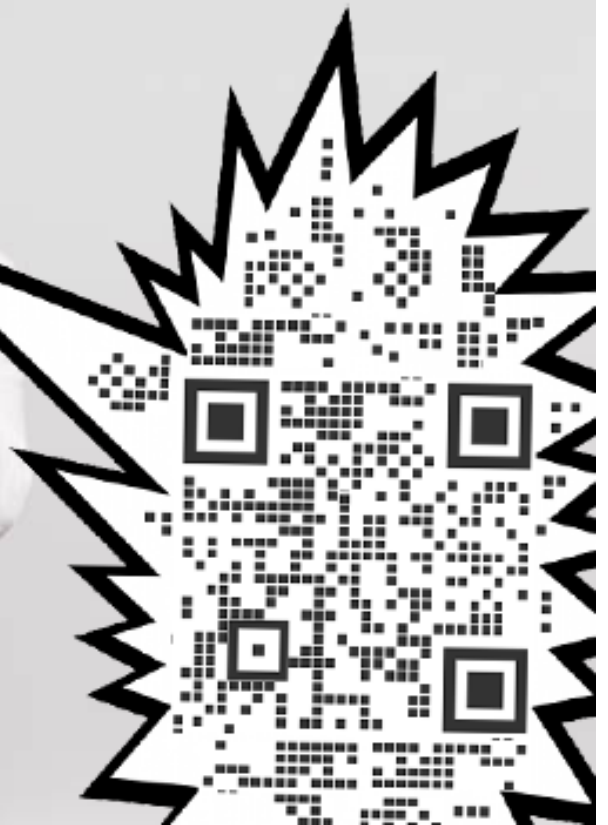


THE BOTANICAL GAZETTE

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THE
BOTANICAL GAZETTE

EDITOR

JOHN MERLE COULTER

VOLUME LI

JANUARY-JUNE, 1911

WITH TWENTY-NINE PLATES AND FORTY-SEVEN FIGURES

MO. BOT. GARDEN
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ERRATA

P. 183, citation 29, for **51** read **52**.

P. 290, last line, for "a face of" read "face of a."

P. 364, line 5, strike out (5).

af 73

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January 1911

Editor: JOHN M. COULTER

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Briefer Articles

Ergot on Oats C. W. Warburton

Current Literature

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Issued January 17, 1911

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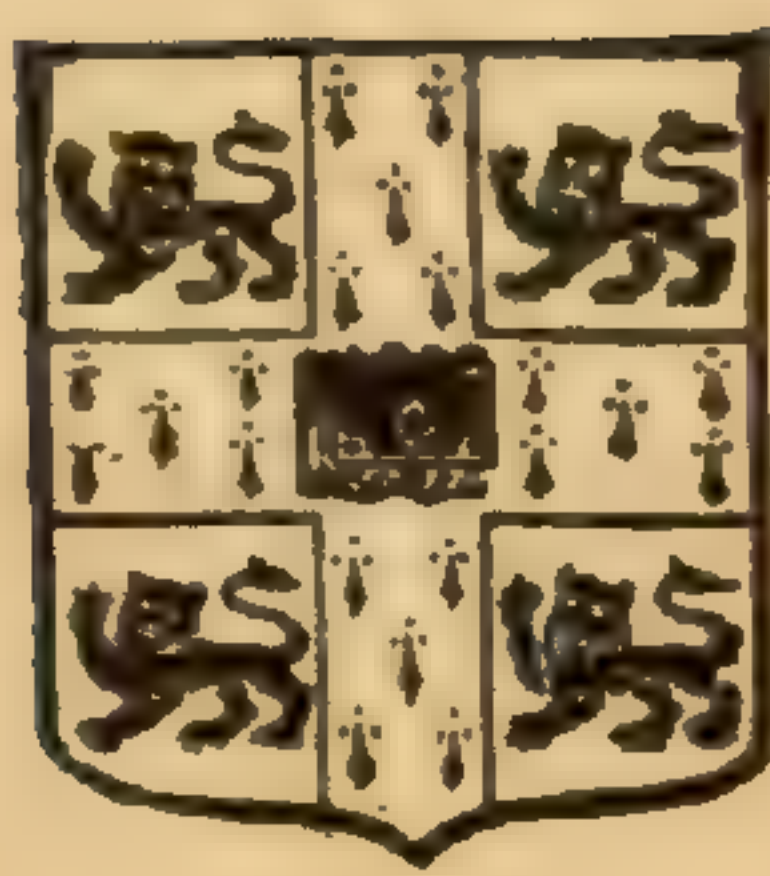
JOHN M. COULTER AND CHARLES J. CHAMBERLAIN

IN 1901, Coulter and Chamberlain published their "Morphology of Gymnosperms," which brought together in organized form the results of research up to that time. The book was based partly on original work by the authors and partly on material from the reports of other investigators, and it at once took its place as the standard work on the subject.

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ANNOUNCEMENT BY
THE UNIVERSITY OF CAMBRIDGE (England)
IN ALL ENGLISH-SPEAKING COUNTRIES
IN REGARD TO THE NEW (11th) EDITION OF THE
ENCYCLOPÆDIA BRITANNICA

The new (11th) Edition of the *Encyclopædia Britannica* (in 28 volumes and Index), which has been in preparation for eight years, is in the printers' hands, and advance subscriptions will now be accepted, but no remittance need be sent until after delivery. This new work, which will be published by the University of Cambridge, will embody certain new features as regards its literary contents, editorial plan, and format, which it is the purpose of this announcement in the United States and Canada, and of similar ones in Great Britain, Australasia, India, and elsewhere, to make public at the same time.

THE first edition of the *Encyclopædia Britannica* was issued in 1768-71, and the last completely new edition was the Ninth, issued in 25 volumes between 1875 and 1889.

The reputation and authority of the *Encyclopædia Britannica* have for many years been household words in all English-speaking countries. To affirm that its authority has always been acknowledged with frank and unqualified acceptance by all intelligent persons is to state no more than the literal truth. Its long career as the most comprehensive work of reference has given it, during 140 years of continuous existence, a pre-eminence which has never been approached—and appears to be unapproachable. In its own way it stands forth so conspicuously that no other book in any language can be compared to it. Regarded from the point of view of a vast literary monument erected by scholars, each successive generation adding to it, strengthening it, perfecting it, broadening its foundations and widening its proportions, it has come to possess a character and a dignity all its own.

The last completely new edition (the Ninth) was built on lines of greater comprehensiveness than any of its predecessors, and its literary contents reached a higher level of excellence than had previously been attained. It represented the point of view of the

'eighties. Since then, the progress of discovery and the application of the scientific spirit to every branch of activity have resulted in a virtual reconstruction in the premises and conclusions upon which a large part of the knowledge of that day was based. It is not necessary here to recapitulate the fields in which this astonishing revolution has been made. The fact remains that a work affording an entirely new and original survey of universal knowledge, constructed on the same lines of comprehensiveness which marked the previous edition, and maintaining its high reputation, was not only necessary—it was inevitable.

Editorial Expenses of the 11th Edition
£163,000 (\$815,000)

THE editorial cost alone—the sum paid to contributors, editors and editorial assistants during the last eight years—has been £163,000 (\$815,000), more than twice the sum (£60,000) similarly expended for the ninth edition. Nearly all the articles in the last edition have been superseded by new ones, and thousands of new headings never before entered in the *Encyclopædia Britannica* have been introduced. In those cases where a fresh survey, in the opinion of experts, could discover no better basis

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for exposition of a subject than the article in the Ninth Edition or its supplement, it has been carried forward with necessary alterations. Of the 40,000 articles in the new edition, 85 per cent. are new, and 15 per cent. are traceable, with changes slight sometimes in extent but often important in quality, to the old work. Thus the University of Cambridge feels justified in asserting with confidence that the new *Encyclopædia Britannica* (11th Edition) constitutes the best and most conscientious treatment of universal knowledge the present day can afford.

The scholars and specialists of the whole world have lent cordial co-operation to the making of the new work; not Cambridge alone, but Oxford, London, Edinburgh, Birmingham, Paris, Berlin, Göttingen, Vienna, Kyoto; and in America, Harvard, Yale, Columbia, Johns Hopkins, Chicago, Pennsylvania, Princeton, Toronto—and many more—the universities and centres of research everywhere have given their ablest minds to the preparation of a new and comprehensive summary of all that is known in every department of human knowledge in 1910.

The 1,500 Contributors

THE quality of utility, an attribute of the *Encyclopædia Britannica*, the attainment of which has been the inspiring motive of the editors ever since the inception of the work in 1768, is inseparable from authority. There is but one method of assuring to any work of reference this essential authority—the employment of the services:

(1) of *men of learning*—original scholars who formulate great principles or develop important discoveries or master some one subject to which they have devoted special and long-continued investigation. In this class are university professors, scientists, philosophers, divines, historians, economists—independent thinkers who are themselves the source from which all that is known of a subject flows as a stream from its fountain-head.

(2) of *men of action*—soldiers, sailors, men of affairs, jurists, administrators, architects, surgeons, artists, inventors, explorers, engineers, sportsmen, manufacturers, financiers—the men who apply their knowledge to constructive results in the every-day pursuit of their profession or vocation; and

(3) of *practical experts* who are engaged in the advancement of industrial undertakings for the welfare of mankind. The *Encyclopædia Britannica* being first and last a repository of all knowledge, it is just as essential to its completeness and authority that it should give practical information about road-making, bridge-building, and ship-building, as that it should

contain treatises on astronomy and geology—it should instruct the reader on oil-engines and the boring of oil wells and on the practical side of forestry, on the making of glass or paper, and on carpentry, not less intelligently than it expounds the Copernican theory and the philosophy of Hegel. As a matter of fact, what the general reader most often looks for in his encyclopædia is just this sort of practical information—information which, it may be, he can turn to immediate profit, but cannot obtain from any other source. On its purely practical side—the massing of exact knowledge covering every kind of activity to which the genius of modern industry has been directed—the new *Encyclopædia Britannica* is a veritable storehouse of the latest information, the Editors having been not less careful in selecting the leading experts to write articles of a utilitarian character than in choosing writers of articles of a purely theoretical sort.

New Features of the New Encyclopædia Britannica

In this connection, it will be interesting to note in what respects the new (Eleventh) Edition to be issued by the University of Cambridge will be distinguished from the last edition, and to indicate where there has been an improvement.

1. For the first time a university will issue an encyclopædia, an adequate and up-to-date exposition of all human knowledge, an authoritative and comprehensive survey of human thought, learning, and achievement. Private enterprise has hitherto been responsible for the issue of the *Encyclopædia Britannica*; but its position to-day as a potent instrument of popular culture, and the intimate association with its literary production of the foremost university professors and specialist authorities of England, the United States and Europe, have given it finally the character of an international institution—a heritage of English-speaking people in every part of the world. The scholarship of the university is, in the last analysis, the inspiring force that has supplied the impetus—in science, in discovery, and in commerce—to which the wonderful expansion of our race is due. It is, therefore, peculiarly fitting that this great library of universal knowledge should be issued now and henceforth by the University of Cambridge, an ancient public institution whose leadership in the world of science is unquestioned.

Cambridge, moreover, has been for many years associated with the University Extension movement, having for its object the diffusion of knowledge outside the circle of mere students. The issue of the new *Encyclopædia Britannica* (11th Edition) is another step in the direction of extending the influence of the University beyond academic or local limits.

THE ENCYCLOPÆDIA BRITANNICA (11th Edition)

A Work of International Scholarship

2. For the first time the *Encyclopædia Britannica* will be issued as a joint undertaking on the part of the most competent authorities without regard to country. The new edition is, in fact, a work of international scholarship. In a large sense, the whole civilised world is now one in thought, in intellectual sympathy, and in aspiration. There is a closer communion of scholarly aims and a readier acceptance of the achievements of other countries than ever before. The Editors, therefore, approached their task in no merely insular spirit, but in the spirit which recognises that scholarship to-day knows no nationality. The 40,000 articles in the work have been written by some 1,500 contributors, representing the highest scholarship and the best practical knowledge of the twentieth century, wherever these can be found. In pursuance of this policy, not only British, but the leading American, French, German, and Italian authorities were invited to contribute. Every article in the new (Eleventh) Edition of the *Encyclopædia Britannica* has therefore been written by a first-hand authority, irrespective of whether he happens to live in Great Britain or her Colonies, in the United States, Germany, France, Japan, or any other civilised country. Two cases in point may here be cited: The articles on Mahommedan Institutions and Mahommedan Law (notwithstanding the fact that the British Empire has more Mahommedan subjects than any other country) come from the Hartford Theological Seminary, being the work of Professor D. B. Macdonald, admittedly the best authority on these subjects, and the chapter on the history of ancient China is the work of Professor Hirth, of Columbia.

Continuous Editorial Control

3. For the first time the contents of the *Encyclopædia Britannica* have been written simultaneously, so that the entire work has been under the Editor's view continuously, the first volume being no less recent in its information than the last. They are therefore being printed, and will be delivered to subscribers at practically the same time, instead of, as in the past, volume by volume.

The old piecemeal method of producing an encyclopædia prevented the Editor from exercising control equally upon all parts of it. In the case of the Ninth Edition, the interval between the publication of the first and the twenty-fifth volume was 14 years. In the case of the new (Eleventh) Edition of the *Encyclopædia Britannica*, practically the whole of the work has been under the Editor's view before a single volume has been sent to press, thus enabling him to give not less recent attention to the "A" volume than to the "Z" volume, to ensure that the article on Archi-

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ture should be as up to date as the article on Zoology, and, finally, to allot the space under all headings according to their importance, without undue emphasis on any one. All of the volumes, therefore, are of an even date (1910). The Editors have, further, by the method of continuous control, been able to eliminate repetitions and inconsistencies, and to prevent overlapping. The information under each heading is complete and individual, and does not appear elsewhere even in a different setting. A serious defect of the last edition has in this way been obviated. The new edition, as a matter of fact, contains more than twice as much information as the Ninth.

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5. The decision to effect a wide departure from the principle of comprehensive treatment at the sacrifice of lucidity has enabled the Editors to help the reader in another way. Unfamiliar words, especially those of a scientific character, or having to do with the investigations of specialists, are explained either under their own headings after the manner of a dictionary or in the body of the text as they occur. So convenient an expedient, one so welcome to the truthseeker, did not occur to the editors of previous editions, though it was estimated at the time the Ninth Edition appeared, that it contained 10,000 strange words not to be found even in the largest English dictionary. The new edition of the *Encyclopædia Britannica* explains thousands of technical terms and new words that the progress of science and discovery has introduced within recent years, as well as all older words, which have an interesting history or a complicated meaning.

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BOTANICAL GAZETTE

JANUARY 1911

THE ORIGIN AND TAXONOMIC VALUE OF THE "VEIL" IN DICTYOPHORA AND ITHYPHALLUS¹

GEO. F. ATKINSON

(WITH PLATES I-VII AND ONE FIGURE)

Although *Ithyphallus impudicus* is quite common and widely distributed in Europe, a complete and satisfactory account of its development, which is sufficient for a full comparison with other related plants, has not yet been given. This is probably due to the fact that it is very difficult to find a sufficiently large number of good specimens in the young stages of development. The more recent and most nearly complete accounts are those by ED. FISCHER (6, p. 22; 7, p. 12) and VAN BAMBEKE (17-21). The gross structures in the later stages of development had already been described by ROSSMAN (14, p. 185) and by DEBARY (3, p. 203), but FISCHER studied the principal features in the origin and development of the parts within the undifferentiated fruit bodies, from the time when they first make their appearance on the rhizomorphs as minute undifferentiated structures, only a few millimeters in diameter, up to their complete differentiation.

Notwithstanding the valuable results which are presented in these contributions, there still remain some questions concerning which there is a difference of statement and opinion as expressed by several students and writers on the Phallales. These questions relate to the very early origin and differentiation of the fruit body,

¹ Contribution from the Département of Botany of Cornell University, no. 138.

NOTE.—Investigation prosecuted with the aid of a grant from the Botanical Society of America in 1905.

and especially to the origin and homology of the so-called "veil," which is described in some species but is often regarded as absent in others. For example, a rather persistent membranous "veil" is described in *Phallus ravenelii* B. and C., an evanescent membranous veil in *Ithyphallus tenuis* Ed. Fischer (PENZIG 13, p. 146), while *Ithyphallus impudicus* is often regarded as wholly lacking a veil at the time of the expansion of the plant.

This study was undertaken with the purpose of answering, if possible, some of these questions. It naturally led to a study of the origin of the veil in *Ithyphallus impudicus*, and to a comparative study of this structure in *I. impudicus* with the "veil" in *Phallus ravenelii* B. and C., and the "indusium" in *Dictyophora duplicata* (Bosc.) Ed. Fischer; and to a consideration of the generic value of these structures.

While studying and photographing the fungi of France in the vicinity of Pontarlier, France, and other villages in that section of the Jura Mountains, I had an opportunity of collecting considerable material of *Ithyphallus impudicus* in different stages of development. Several individuals were first found and collected by my friend M. A. COURTET,² who accompanied me on many of the excursions, and showed me the locality where this plant was growing. It was in a forest by the roadside, and the plants were growing for some distance around an old decaying stump. In the vicinity of some of the rotten wood, strands of the mycelium were found with numerous very young fruit bodies. Others were found which were older, thus presenting an interesting series of development from the very young and minute fruit bodies to the mature plants (text fig. 1). As many as possible of these were collected in different stages. Not having any other fixer at hand, they were fixed in alcohol and picric acid, and then preserved in 75 per cent alcohol.

In the very early stages of the development of the young fruit bodies, their structure corresponds very closely with that of the growing end of the rhizomorphs as described by DEBARY (3, p.

² M. Courtet is professor of mathematics at the Lycée in Besançon, but resides in Pontarlier, where he spends his vacations, and is a member of the Soc. Myc. de France.

203), and later by FISCHER (6, p. 23). These rhizomorphs consist of a central strand or core, and a cortex. The central strand or core is composed of hyphae, the general direction of which is parallel with the axis, while here and there certain hyphae turn outward with the cortex. Between the hyphae there is more or less gelatinous substance, which is more abundant in the central portion of the core, where the threads are rather distant, while on its periphery they are more crowded. These threads stain readily, so that



FIG. 1.—Rhizomorphs and young fruit bodies of *Ithyphallus impudicus*, from Pontarlier, France, 1905; natural size.

in longitudinal sections this medulla or core stands out distinctly from the rather thin cortex.

In the young fruit bodies, according to FISCHER (6, p. 23), this medulla is present and terminates in a tissue of slender hyphae which are rich in protoplasmic content. This central portion of the pyriform young fruit body has the form of a sheaf, which in longitudinal section presents a fan-shaped outline. This tissue also stains readily and is surrounded by a cortical layer of looser texture, the external portion of which contains hyphae and crystals of calcium oxalate, exactly like those in the cortex of the rhizomorphs. BURT (1a, p. 347) describes a similar structure in the young fruit bodies of *Mutinus caninus* (Huds.) Fr., but differs from

FISCHER in regard to the part which the central core or medulla plays in the formation of the mature fruit body. According to FISCHER, the wall of the "stipe" (the stemlike portion of the receptacle) is formed on the outside of the portion of the medulla which lies within the young fruit body, so that this portion of the medulla or central strand would lie within the stipe. According to BURT, in *Mutinus caninus* the central strand, while connected with the central mass of tissue in the young fruit body, does not take part in the formation of the stipe. All parts of the fruit body, with the exception of the external portion of the outer layer of the volva, are, according to him, derived from the deeply staining mass of tissue which lies in the center of the broadened end of the young fruit body. The examination which I have been able to make of longitudinal sections of young fruit bodies of *Ithyphallus impudicus*, in the different stages of development, leads me to believe that the position and extent of development of this central strand in the young fruit bodies is a variable one.

In the center of the broadened end of the very young fruit body there arises a homogeneous, compact tissue, composed of intricately interwoven hyphae rich in protoplasm. This tissue may be regarded as fundamental or primordial tissue, which later gives rise by growth and differentiation to the parts of the mature plant. In none of the very young fruit bodies, just prior to or at the time of the appearance of this central primordium, of which I succeeded in getting longitudinal sections, was there a direct continuation of the central strand into the middle portion. The hyphae of the central strand, singly or in fascicles often fan-shaped, diverge in various directions and seem to be lost near the periphery of the proximal end. The central portion of the young fruit body is probably developed from the young apical region of the central strand, but in none examined have I seen the strand as a whole in connection with the central primordium, or, as already stated, even extending into the central region of the young fruit body. My sections have been studied very carefully in this respect, since BURT in *Mutinus caninus* and FISCHER in *Ithyphallus impudicus* have found the strands as a whole extending into the interior of the fruit body, and as a whole in connection with the central

primordium. The failure to find it in this connection in the specimens examined by me is not to be taken to mean that in some or in many specimens it is not so connected with the central primordium, but rather lends support to the view held by BURT that the medulla of the rhizomorph, when it does extend into the center of the young fruit body, is not concerned in the organization of the members of the mature plant, but that these are organized from the central primordium.

The first evidence of the differentiation of the primordium is the gelatinization of the hyphae in the extreme upper portion just inside the cortical layer. This occurs in a small circular area which progresses centrifugally and downward from its edge, so that it becomes at first convex (fig. 17), and later campanulate, as it extends downward on all sides in the area, occupying the same relation to the central primordium and cortex. This forms the thick gelatinous middle layer of the volva. In the early stages of this gelatinous area, the swelling of the gelatinous substance, formed from the outer layers of the hyphae, crowds the hyphae apart and they form an irregular open network with large, more or less rounded gelatinous masses in the mesh. But with the formation of more of the gelatinous substance and the broadening of this layer, many of the hyphae are stretched in a radial direction, extending from the tissue which later forms the inner layer of the peridium (figs. 19-22).

While the development of this gelatinous layer is progressing, and soon after its inception, the fundamentals of other parts begin to make their appearance. The fundament of the stem appears in longitudinal section (figs. 18, 19) as a delicate columnar structure. The central portion of this structure consists of primordial or fundamental tissue, which is but little colored by the stain, while the fundament of its wall stains deeply and extends nearly up to the apex of the bell-shaped structure inside of the gelatinous layer. The bell-shaped area adjacent to the inner surface of the gelatinous layer, which takes a deep stain, is to form the inner wall of the peridium (*D*, figs. 19, 21). Lying directly next to this on the inner side is the fundament of the gleba (*G*, fig. 19), also a bell-shaped area, but not yet differentiated from the former.

Farther within (*P*, fig. 19) is another bell-shaped area which takes a deeper stain than the fundamental tissue on either side. This is the fundament of the inner portion of the pileus.

The remaining primordial tissue lying between the fundament of the pileus and that of the stipe is in the form of a hollow cone, the wall of which is broad at its base. It is the tissue which DEBARY (3, p. 204) called the cone (*Kegel*). In the stained section, a photograph of which is represented in figs. 18, 19, this cone of primordial tissue does not show a homogeneous structure. At *I* there is a deeply stained area, also campanulate in form when taken as a whole, lying within the lighter colored portion of the cone. This is what I regard as the fundament of a true indusium, which in *Ithyphallus impudicus* does not become further differentiated, so far as present evidence indicates, though the rudiment may persist in a recognizable form (in magnified section) up to the maturity of the plant. The hyphae here are somewhat more densely interwoven, and therefore this zone stains more deeply in contrast with the other primordial tissue on either side of it. This rudiment of an indusium described by FISCHER (6, p. 26) remains in the condition of primordial tissue, which, with some adjacent primordial tissue, in the mature plant forms a thin membrane lying between the pileus and the stipe. My interpretation of the fundaments represented by these more deeply staining cones in the young fruit body of *Ithyphallus impudicus* is slightly different from the interpretation given by FISCHER. The zones in fig. 19 indicated by *P* (pileus fundament), *I* (indusium fundament), and *B* (primordial tissue lying between) are considered by FISCHER as one zone, the fundament of an indusium which he marks in his figures as *I*. An examination of his figures shows that it is made up of three layers or zones, two outer ones more deeply stained than the inner one, corresponding to the three zones of my figure (*P*, *B*, and *I*). FISCHER states that the outer layer of his zone *I* forms the inner layer of the pileus, and that the indusium in *Dictyophora phalloidea* Desvaux is differentiated along the inner layer of the zone *I*. Zone *I* of my figure joins the stem at the same place as the inner layer of FISCHER's zone *I*, and also in the mature fruit body, as will be shown later, the zone *I* of my

figures can be distinguished as a more deeply staining layer within the thin membrane of primordial tissue lying between the stipe and pileus, joining the stipe at the projecting ring of the same near the apex of the stipe at the corresponding point where the indusium of *Dictyophora duplicata* joins the stem. These facts lead me to believe that the fundaments represented by the more deeply staining zone in the young fruit body should be interpreted in accordance with their treatment here.

Another peculiar structure sometimes appears at this stage. It lies in the lighter colored zone (figs. 19, 20), and in stained longitudinal sections appears as a delicate line, deeply stained, lying some distance from the fundament of the stem wall, but diverging from it and not presenting the curved contour of the other zones. The walls of the hyphae appear to be slightly gelatinized or thickened and take the stain deeply. Perhaps it represents the beginning of a partial degeneration of the fundamental tissue which does not take part in the formation of any of the members of the plant. Or it may represent a very slight tendency to the formation of the pseudoparenchymatous tissue of an indusium such as exists in a well developed form in *Dictyophora*, since this structure lies close to the fundament of the indusium.

The fundament of the gleba now gives rise upon its inner face to a palisade layer of slender clavate cells. This layer, as it progresses, develops unevenly, forming numerous folds, with furrows between them, which branch profusely as they extend inward toward the forming pileus. Figs. 19 and 21 are from a section, nearly longitudinal, which shows the partially developed members of the plant; *D* is the inner peridium of the volva, *G* is the developing gleba, *P* is the forming pileus, *A* is the apex of the stipe, while *I* is the fundamental tissue between the stipe and pileus. At maturity this fundamental tissue lies between the stem and pileus as a thin, delicate, membranous layer, which also extends below the pileus around the lower end of the stipe. This is undifferentiated tissue. As the stem elongates and the pileus expands somewhat, this delicate membrane or "veil" is torn and fragments are left on the surface of the stem, and occasionally some of them on the inner surface or margin of the pileus. These fragments often

lie around the stem a short distance below the margin of the pileus in the form of a ring (fig. 1). It is so delicate that it collapses, dries, and disappears very soon after the expansion of the plant, or is washed away by the rains, so that it is probably rarely seen except by those who collect the mature "eggs," and in a protected place observe the unfolding of the plant.

The delicate and evanescent character of this "veil" may account for the fact that it is rarely shown in connection with illustrations of this species after expansion, especially in works of a general character. This has probably led to the rather widespread belief, especially in some quarters, that a "veil" is wanting in *Ithyphallus impudicus*. The variability in the strength of this "veil" in individuals of the same species, and in different species, as well as the presence of the indusium in *Dictyophora*, occupying a similar position between the pileus and stem, though of a different structure and ontogenetic history, has led to considerable confusion regarding its nature, origin, and taxonomic value. Many writers have used the terms "veil" and "indusium" synonymously. If the word *velum* or "veil" were used to designate the remnant of primordial or fundamental tissue lying at maturity of the plant between the pileus and stem, and if the word *indusium* were reserved for the organ of different structure which is differentiated and developed from a portion of and within this primordial tissue, it should serve to clear away the existing confusion. A comparison of these structures and a consideration of their origin and later history in *Ithyphallus impudicus*, *Dictyophora duplicata*, and *Phallus ravenelii*, with photographs of stained sections, together with a discussion of some of the literature of the subject, it is hoped will lead to a more intelligent understanding of their nature and taxonomic significance than can be obtained from an examination of them at the time of the expansion of the plants.

Ithyphallus impudicus is a rare plant in the northeastern part of the United States. I have never seen a specimen from this region. *Dictyophora duplicata* is rather common, however. Its size and form, as well as the surface of its pileus, are so similar to *I. impudicus* that, as BURT (1b, p. 384) remarks, there is danger

of mistaking the two in the younger stages, while the indusium remains adherent to the under surface of the pileus before the intervening primordial tissue is ruptured. In old plants after expansion, when the indusium has fallen away, as frequently happens, there is danger of confusing it with *I. impudicus*. *Phallus ravenelii* is also sometimes mistaken for *I. impudicus*, but this should not happen when one is familiar with the character of the pileus in the two species, and with the very different odors of the two.

The first time that I met with growing examples of *Ithyphallus impudicus* was in September 1903, when in company with Mr. GEORGE MASSEE I found two mature eggs in the Kew Gardens. These were taken to the Jodrell Laboratory and placed under a moist chamber. During the night one of them expanded, and on the following day there was very clear evidence of a thin, white, membranous veil between the stem and pileus, which was now lying on the stem a short distance below the pileus and partly encircling the stem as a ring. I photographed the plant at the time, and the presence of this veil is very distinctly shown as a complete membranous ring around the stem (figs. 1, 2). The plant was then placed in alcohol, shipped by freight to this country along with other fungi, and it is now stored in alcohol in a museum jar in the Department of Botany in Cornell University, and shows well at the present time this thin, membranous veil.

In August 1905, in the Jura Mountains at Pontarlier, France, I reared several plants in moist chambers from mature eggs. In all of these the veil was present and adhered either as fragments or as a ring on the stipe. Sometimes also fragments clung to the margin or under surface of the pileus. Several photographs were made of these and one is shown in fig. 2. It is interesting to note in this photographic reproduction the collar around the stipe below, which is the lower remains of the veil where it is attached to the broader remnant of primordial tissue. This is exactly the same structure that is present at this stage in *Phallus ravenelii*. Dissection of the eggs can be made also in such a way as to show a distinct, thin, membranous veil between the stem and pileus before expansion (fig. 8). The veil thus separated from the two

adjacent surfaces of contact stands out clearly, and is continuous from its attachment with the primordial tissue at the base of the stem and volva below to the apex of the stem at the point where the latter joins the pileus.

While, as previously stated, there is quite a widespread belief that a veil is wanting in *I. impudicus*, there is abundant evidence that it was observed by the earlier students of these plants. CORDA (2) figured and described it as early as 1842. His figs. 1, 2, and 3 show a thin veil. He calls it outer stem veil (*äussern Strunkeschleier*³). DEBARY (3, p. 207) speaks of it as a thin, white membrane between the pileus and stem, which is torn into fragments as the stem elongates. His language⁴ shows that various authors spoke of it as a veil (velum), and he himself uses the term after the expansion of the plant, when fragments of it cling to the stem. KALCHBRENNER (8a, p. 63) describes and figures it as present in *Phallus imperialis* Schulzer, which is but a form of *I. impudicus* (see ED. FISCHER 6, p. 84). FISCHER (6, p. 27) describes it as a hyphal weft between the stem and pileus in the mature egg. He regards it as a remnant of the primordial tissue, but does not speak of its appearance after the expansion of the plant. BURT (1b, p. 384) says that the veil is wanting in *I. impudicus*. In his characterization of the genus *Ithyphallus* he says "veil wanting." By this he probably means that a persistent, entire veil, such as is usually present in *Phallus ravenelii*, is wanting in the genus *Ithyphallus* as interpreted by him.

In *Phallus ravenelii* the veil is usually persistent, is composed of a thicker hyphal weft of primordial tissue, and is therefore not so easily torn into fragments, but persists as a campanulate, membranous collar suspended around the stem under the pileus from

³ "Im geschlossenen Eie zwischen dem Hute und dem Strunke eine feine, weisse, zarte Haut, emporschicht, welche den äussern Strunkeschleier (fig. 1¹) bildet, welche bei Verlängerung des Trägers zum Steile, zerreisst, und dessen zarte Fragmente bald verschwinden."—*Icones* 5:71-73. pl. 7. figs. 1-3. 1842.

⁴ "Sie erhält zuletzt die Gestalt einer dünnen weichen Haut welche von den Autoren der Schleier (velum) des Stiels genannt worden ist. . . . Der Kegel reisst in seinem untersten Theile quer durch; die mit dem Basalstücke zusammenhängende Portion bleibt mit letzterm als eine die Stielbasis umgebende napfförmige Scheide stehen; der obere Theil zerreisst in unregelmässige Fetzeln, welche theils zwischen Hut und Stiel, theils auf der freien Aussenfläche des letzteren hängen bleiben (velum)."

the point of their junction. For this reason it is apt to be overlooked unless one is careful to look between the pileus and stem, or unless a section of this part of the plant is made. Sometimes the veil is torn into a few fragments, and at other times it may become free from its point of attachment and lie as a ring or band of membranous tissue around the stem below the pileus. It is then quite plainly seen. This is shown in the photograph reproduced in fig. 5. This figure also shows the membranous collar around the base of the stem with which the veil was connected before expansion of the plant, when it was torn apart.

In the first published description of *Phallus ravenelii* B. and C. (1, p. 33) no mention was made of the presence of this veil. FARLOW (4, p. 247) describes it and speaks of it as a rudiment of a veil. PECK (12, p. 123) also describes and figures it. He speaks of it as an indusium or veil, and states that RAVENEL, on whose notes and specimens BERKELEY described the plant, had made a complete description of this veil in his notes, which BERKELEY failed to include in his description. MORGAN (11, p. 146) places *P. ravenelii* in *Hymenophallus* (as a subgenus of *Phallus*) along with *P. duplicata* Bosc. (*Dictyophora duplicata*), thus considering it more closely related to the present *Dictyophora* than to *I. impudicus*, which he places in *Ithyphallus* (as a subgenus of *Phallus*). In this respect he followed GERARD (8, p. 11). He speaks of the veil as an indusium or veil which is reticulate in some species of *Hymenophallus*, and not reticulate in others, and is dependent from the apex of the stem underneath the pileus. In *Ithyphallus impudicus* he recognizes the thin membrane between the pileus and the stem which is torn into shreds as the plant expands.

ED. FISCHER (6, p. 30) placed *P. ravenelii* in the genus *Ithyphallus* because he believed a true indusium, homologous with the indusium of *Dictyophora*, was absent. In the study of a few young fruit bodies he finds (7, p. 16) not only no evidence of a true indusium in the primordial tissue between the stem and pileus, but also no evidence of a fundament or the beginning of a differentiation of tissue which would indicate a rudimentary indusium. BURT (1b, p. 385) regards the veil in *P. ravenelii* as homologous with the indusium of *Dictyophora*, probably being influenced more by

its usual persistence as a distinct membrane than by its ontogenetic history, though he states (1b, p. 386) that some laterally inflated toward hyphae led him to believe that this indicates a differentiation pseudoparenchymatous tissue. SCOFIELD (15, p. 533) does not consider the veil in *P. ravenelii* to be a differentiated organic structure, but a remnant of the tissues of the young fruit body. Consequently he follows FISCHER in placing the species in the genus *Ithyphallus*. It appears that LLOYD (9, p. 327) treats the indusium of *Dictyophora* and the veil of *Ithyphallus*, even the very thin and fragile veil of *I. impudicus*, as homologous structures, probably without a consideration of their different origin and ontogenetic history, since he thinks "the only difference is in the degree of development of the veil." On this basis he would discard the genus *Dictyophora*, and place all three of the species in question here in the genus *Phallus*.

There are two methods by which the relative value of these structures (the "veil" and indusium) in showing generic relationship may be considered: (1) by their morphology, that is, their form, structure, and position relative to other organs of the plants; and (2) by their origin and differentiation in the individuals, or in other words their ontogenetic history. According to the first, it is not sufficient that we should compare these structures after the expansion of the plant. Some of the present confusion probably can be traced to observations made only at this stage of development. Observations and comparisons should also be made before the elongation of the stipe has so disarranged the parts as to make impossible a careful comparative study of these structures in their normal position. For the purpose of this study fruit bodies of the three species (*I. impudicus*, *P. ravenelii*, and *D. duplicata*) were selected a short time before complete maturity, but after complete differentiation of the parts had taken place, and only a comparatively short time before the period of elongation. Microtome sections were made of these, longitudinally at the upper and lower ends of the "egg," and transversely as well as longitudinally in the middle region. These sections included the volva, pileus, and one side of the stipe (to or near the middle), and of course the tissues in question between the pileus and stipe, and the base of

the volva. These were stained, mounted in balsam, and then photographed at various magnifications, as indicated in the description of the plates. They were also subjected to careful microscopic study.

It will be interesting to study the figures here reproduced from some of these photographs. Figs. 9, 10, 11 are from longitudinal (radial) sections at the base of these three species. Fig. 9 is *Ithyphallus impudicus*, and the parts are as follows (the outer layer of the volva is not shown here): *F*, gelatinous layer of the volva; *D*, inner layer of the volva; *G*, gleba; *P*, pileus; *A*, stem; *B*, primordial tissue. The primordial tissue shows no differentiation. It consists of intricately interwoven hyphae and is a remnant of the primordial tissue of the young fruit body, which has been left behind after the organization of the other parts of the plant. Next the pileus and the stipe there is a slightly darker line, the result probably of a slight massing or distintegration of those hyphae which are crowded by the enlarging stem and pileus. There is no evidence here of the differentiation of another structure within this primordial tissue. At the narrowed portion above is the point near which the primordial tissue is torn apart in the elongation of the stem, separating the thin, membranous part from the broader part below (see fig. 2).

Fig. 10 is of *Phallus ravenelii*. The primordial tissue lying between the base of the stem and the lower part of the pileus also shows no differentiation, the portions next the pileus and stem staining slightly darker, as in *I. impudicus*, and from the same cause. This represents a rather thin veil for *P. ravenelii*, and therefore serves to show, aside from there being no difference in its structure, position, and relation at this point in the fruit body from the veil of *I. impudicus*, that it is not any more massive. A short distance above the margin of the pileus is the point where the veil ruptures, leaving the collar of primordial tissue around the base of the stem as in *I. impudicus*.

Fig. 11 is of *Dictyophora duplicata*. The parts are lettered as in the two previous figures of *I. impudicus* and *P. ravenelii*. We note outer layer of volva; *F*, gelatinous layer of volva; *D*, inner layer of volva; *G*, gleba; *P*, pileus; *A*, stem; and *B*, primordial

tissue. There is here, however, an additional organ, or part of the fruit body, which lies within the primordial tissue, leaving a thin layer of primordial tissue next to the stem and one next the pileus. This is the indusium (*I*), which in this species is composed of chambered, pseudoparenchymatous tissue differentiated from and within the primordial tissue and not extending down into the tissue at the base. The remnant of primordial tissue here is exactly homologous with that which we have just observed in *I. impudicus* and *P. ravenelii*. In this figure there is seen the thin, white membrane or veil which lies between the indusium and the stem, and which is continuous with the more massive area of primordial tissue below. The remnant of primordial tissue between the pileus and indusium is in this specimen, at this point, very thin, but it is present and can be seen extending around below the margin of the indusium to join the other branch where the two veils or membranes pass into the mass of primordial tissue below.

Fig. 12 is of a longitudinal section from *I. impudicus* at the upper end of the fruit body, the lettering as before. Here we should note the inner and outer layers of the main part of the pileus, which in the section stain as dark lines in contrast to the looser tissue of the trama between. The inner wall of the pileus can be here traced upward as a very distinct dark line. For want of space, the entire photograph is not reproduced here, the upper portion being cut away; but the pileus above curves over and is joined with the margin of the stem apex. Between the pileus and the stem is seen the primordial tissue, the "veil." A very interesting structure is present here. Through the middle of the primordial tissue, parallel with the surface of the pileus and stem, but separated from them on either side by primordial tissue, is a darker line, represented by slightly denser tissue which stains darker than that on either side. This is the indusium rudiment described earlier in the study of the development of the young fruit bodies, and it is quite remarkable that this rudiment should persist within the veil up to the maturity of the fruit body, so that it can be recognized in microscopical preparations. It does not continue to the apex of the stem along with the membrane of primordial tissue, but ends a short distance below at the projecting ring in the stem correspond-

ing to the point where it was observed in the younger fruit bodies, and also to the point where the well organized indusium of *Dictyophora* is attached (see fig. 13).

Fig. 13 is from a similar section of *D. duplicata*, that is, a longitudinal section at the upper part of the fruit body; the indusium (*I*) is joined to the stipe at the point where the annular projection occurs. The main portion of the remnant of primordial tissue lies between the indusium and stipe, a very thin layer only lying between the indusium and pileus, which is continuous with the primordial tissue above the indusium between the stipe and pileus. The dark line at the edge of the primordial tissue next the indusium is caused by the denser accumulation of hyphae as they have withdrawn or have been pushed back by the folding and crowding of the chamber walls of the indusium. In this figure can be seen also the delicate weft of hyphae lying in the chambers of the stipe, pileus, and indusium. This is the remnant of primordial tissue within and from which these parts were organized. It is continuous at certain points with the "veil" or membrane of primordial tissue lying between the stipe and pileus and enveloping the indusium. A similar weft of primordial tissue lies within the chambers of the stipe and pileus in the other species.

Fig. 14 is from a longitudinal section in the same region of the fruit body of *Phallus ravenelii*. The "veil" (*B*) is seen to consist of undifferentiated tissue, that is of primordial tissue. There is no evidence of a distinct organ like the indusium of *Dictyophora* lying within it, nor even of a fundament or rudiment of such an organ. The primordial tissue is a homogeneous weft which is continuous between the chambered walls of the stipe.

It will be interesting now to examine cross-sections near the middle region of the fruit body at the same stage of development. *Phallus ravenelii* presents nothing essentially different from that shown in fig. 14; but from a comparison of the photographs of these sections from *Ithyphallus impudicus* (fig. 15) and *Dictyophora duplicata* (fig. 16), the impression is at once gained that in *Dictyophora duplicata*, as represented by this specimen, there is a "veil," in addition to the indusium, quite as strong as that present in *Ithyphallus impudicus*. It is therefore quite possible that, at the

time of expansion of the plant, fragments of a veil are to be found in addition to the well developed indusium. In some examples of *Phallus ravenelii* the "veil" is scarcely more massive than is here represented in *Dictyophora duplicata*. The fact that in *Phallus ravenelii* it is usually more massive and thus more permanent, is not a sufficient ground for considering it homologous with an entirely different organ in other species, which originates within and from a portion of this primordial tissue.

The corresponding cross-section of *Ithyphallus impudicus*, reproduced in fig. 15 from a photograph, is very instructive in this connection. Lying within the primordial tissue and parallel with the surfaces of the stipe and pileus wall is a thin layer of more deeply staining tissue. This is the fundament or rudiment of an indusium, which was observed in the longitudinal section of the upper part of the fruit body, and first appears in the young fruit body at the time of the origin of the fundament of the pileus. It has not advanced beyond the condition of primordial tissue, but the more dense arrangement of the hyphae and their deeper staining reaction is retained, in some examples at least, up to the maturity of the fruit body. As already stated, ED. FISCHER has described and figured the fundament of the indusium in the very young stages of *Ithyphallus impudicus*, although I differ slightly from him as to the limits of this fundament. It is homologous with the corresponding stages of the indusium fundament in *Dictyophora phalloidea* as described and figured by him. In the young stages of *Phallus ravenelii* studied by him (7, p. 15) he found no evidence of even a fundament of the indusium, though the material which he studied did not include the very young stages.

From all that has been determined in connection with this study, however, together with the results of other investigations on these species, the conclusion that a true indusium is wanting in *Phallus ravenelii* appears to be justified. If *Dictyophora* is to be retained as a genus distinct from *Ithyphallus*, as at present I believe it should be, *Phallus ravenelii* cannot properly be placed in the genus *Dictyophora* if the indusium of this genus is to be interpreted in the light of its ontogenetic history and distinct differentiation from primordial tissue, rather than upon the mere fact of the

presence of a campanulate structure more or less persistent and usually but not always suspended between the pileus and stipe, without regard to the important question of its real homology. With regard to the generic position of *Ithyphallus impudicus* the question may arise as to whether or not it should be placed in the genus *Dictyophora* on account of the rudiment of an indusium within the primordial tissue. If a rudimentary condition of an organ were to have the same taxonomic value as the well developed condition of the same organ, *I. impudicus* would be congeneric with the species of *Dictyophora*. But a rudimentary condition of an organ is not generally regarded as of equal taxonomic value with its well developed state in other species, though it may be of value in a study of phylogenetic relationship. *I. impudicus*, therefore, should not be placed in *Dictyophora*, or rather is not congeneric with it, though, curiously, it probably shows a closer phylogenetic relationship to that genus than does *Phallus ravenelii*. *Phallus ravenelii* B. and C. and *Ithyphallus impudicus* (L.) are then to be regarded as congeneric, and if the genus *Ithyphallus* is to be retained, the former should then be known as *Ithyphallus ravenelii* (B. and C.) Ed. Fischer.

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DESCRIPTION OF PLATES I-VII

Magnifications are as follows: figs. 9-13, 18, 22, $\times 10$; figs. 14-17, $\times 25$. Photographs by the author.

PLATE I

FIGS. 1, 3.—*Ithyphallus impudicus* from Kew Gardens, England, 1903; fig. 1 enlarged from kodak fig. 3.

FIG. 2.—*Ithyphallus impudicus* from Jura Mountains, France, 1905, showing "veil" around stem below pileus; at the base showing the collar of fundamental tissue which was ruptured on expansion of plant.

PLATE II

FIG. 4.—*Phallus ravenelii* from Ithaca, N.Y., showing "veil" around stem below pileus; at base showing the collar of fundamental tissue as in *Ithyphallus impudicus*.

FIG. 5.—Same with pileus cut away from the front to show upper part of "veil" suspended from apex of stem underneath pileus; two rings of this "veil" of fundamental tissue below on the stem; at base collar of fundamental tissue.

PLATE III

FIG. 6.—*Dictyophora duplicata*, Ithaca, N.Y., showing indusium.

FIG. 7.—Dissection of egg of *Phallus ravenelii*, showing continuous veil of primordial tissue between pileus and stem.

FIG. 8.—Similar dissection of *Ithyphallus impudicus*, showing continuous veil of primordial tissue between pileus and stem.

PLATE IV

FIG. 9.—Longitudinal radial section at base of egg of *Ithyphallus impudicus*: *A*, stem; *B*, primordial tissue which forms the collar; *P*, inner portion of pileus; *G*, gleba; *D*, inner peridium; *F*, gelatinous layer of volva.

FIG. 10.—Longitudinal radial section at base of egg of *Phallus ravenelii*: *A*, stem; *B*, fundamental tissue which forms the collar; *P*, pileus; *G*, gleba; *D*, inner peridium; *F*, gelatinous layer of volva.

FIG. 11.—Longitudinal radial section at base of egg of *Dictyophora duplicata*: *A*, stem; *B*, fundamental tissue which forms the collar and extends upward as a thin veil on either side of *I* (indusium); *P*, pileus; *G*, gleba; *D*, inner peridium; *F*, gelatinous layer of volva.

PLATE V

FIG. 12.—Longitudinal radial section through upper part of egg of *Ithyphallus impudicus*: *A*, stem; *BB*, fundamental tissue with rudimentary indusium; *I*, indusium lying with it; *P*, pileus; *G*, gleba; *D*, inner peridium.

FIG. 13.—Longitudinal radial section at upper part of egg of *Dictyophora duplicata*: *A*, stem; *BB*, fundamental tissue; *I*, indusium; *P*, pileus; *G*, gleba; *D*, inner peridium; *F*, gelatinous layer of volva.

PLATE VI

FIG. 14.—Longitudinal radial section through upper part of egg of *Phallus ravenelii*: *A*, stem; *B*, fundamental tissue; *P*, pileus; *G*, gleba.

FIG. 15.—Transverse section through middle part of egg of *Ithyphallus impudicus*: *A*, stem; *B*, fundamental tissue; *I*, rudiment of indusium within it; *G*, gleba; fundamental tissue also lies between *I* and *P*.

FIG. 16.—Transverse section through middle part of egg of *Dictyophora duplicata*: *A*, stem; *BB*, fundamental tissue lying on either side of *I* (indusium); *P*, pileus; *G*, gleba; *D*, inner peridium; *F*, gelatinous layer of volva.

PLATE VII

Ithyphallus impudicus from Jura Mountains, France; sections showing different stages in development of young fruit bodies.

FIG. 17.—Very young fruit body showing gelatinous area near the apex; the dark area is the fundament of the fruit body.

FIGS. 18–22.—Older stages showing early differentiation of parts of fruit body: *A*, stem; *I*, rudimentary indusium; *P*, pileus; *D*, inner peridium; *G*, gleba.

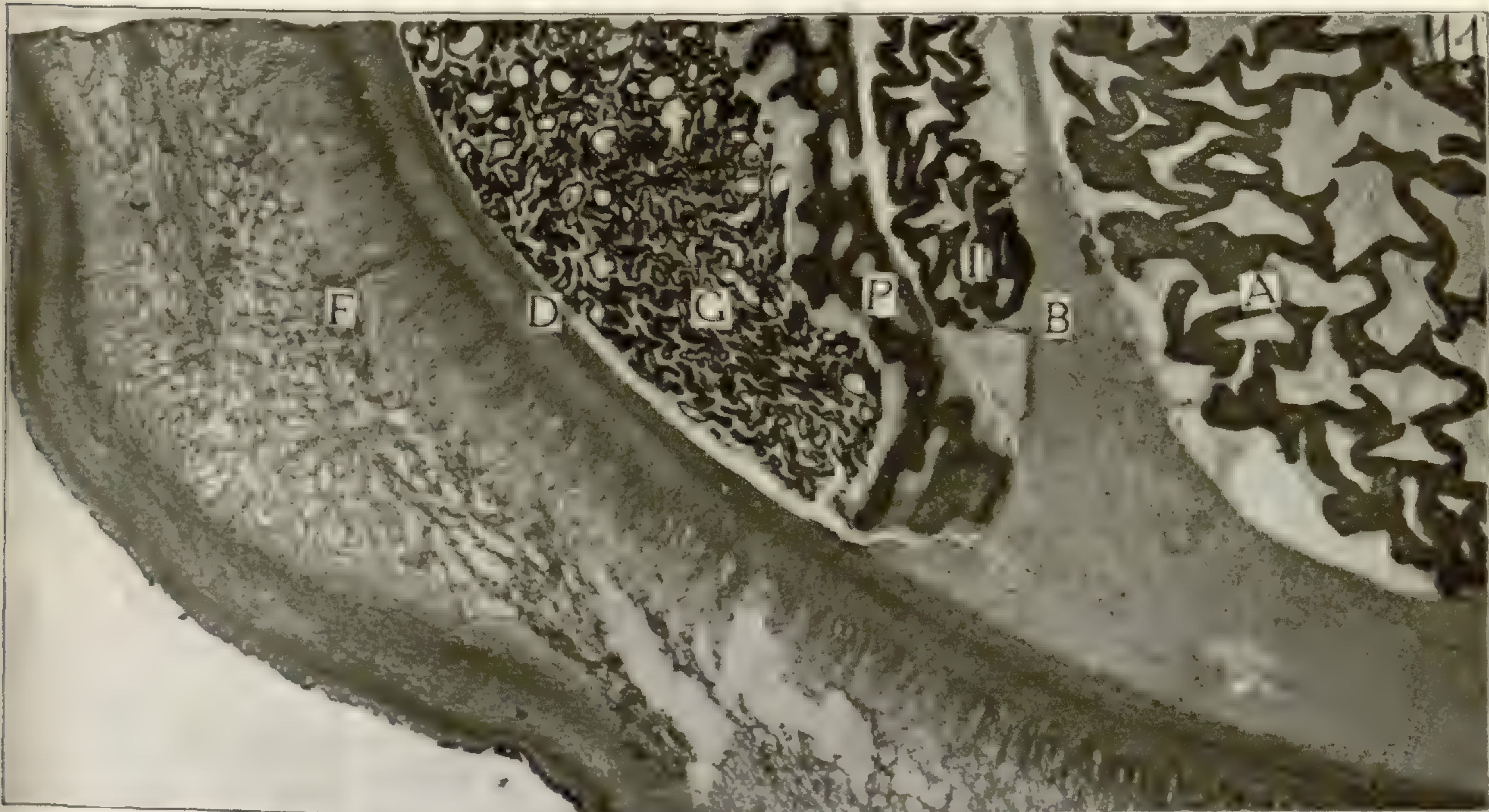
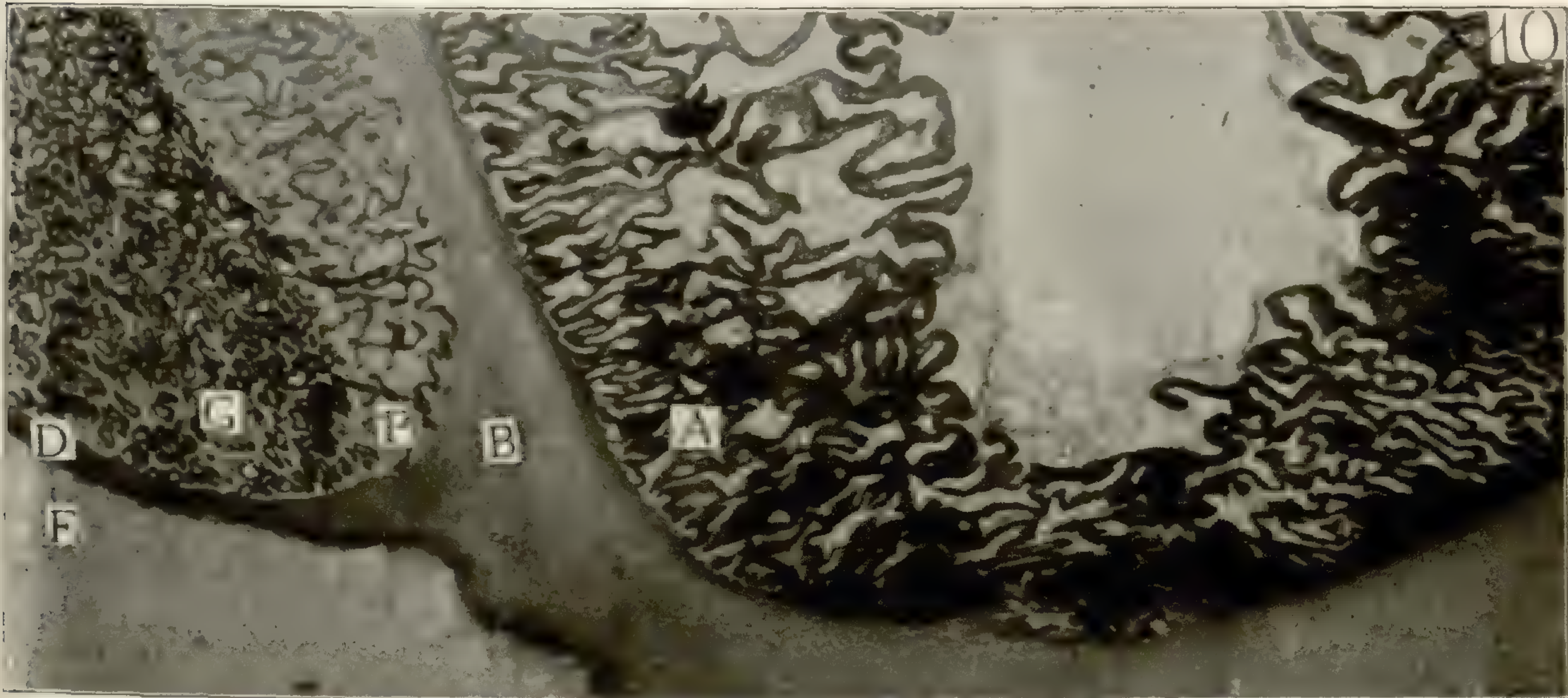
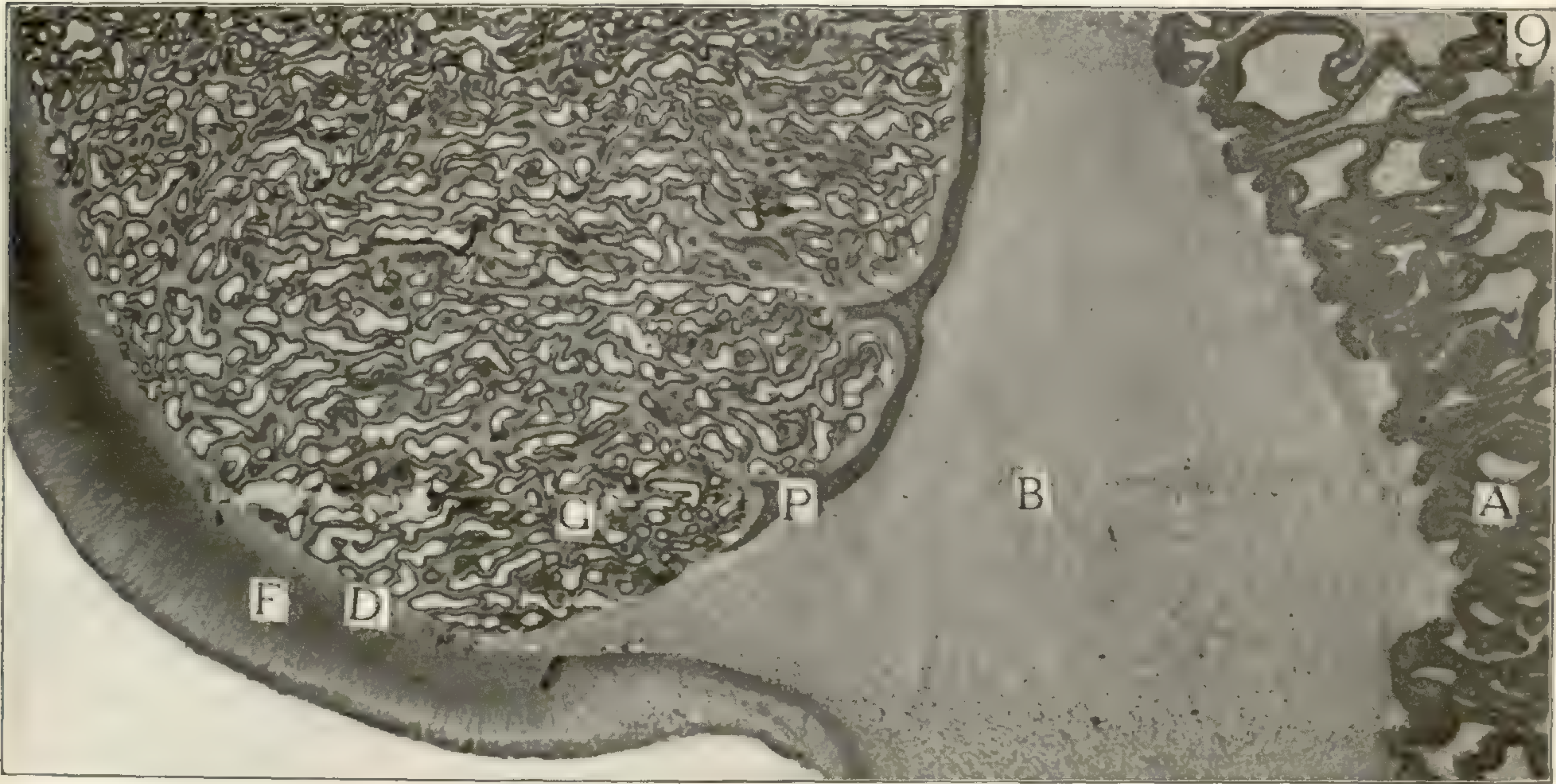


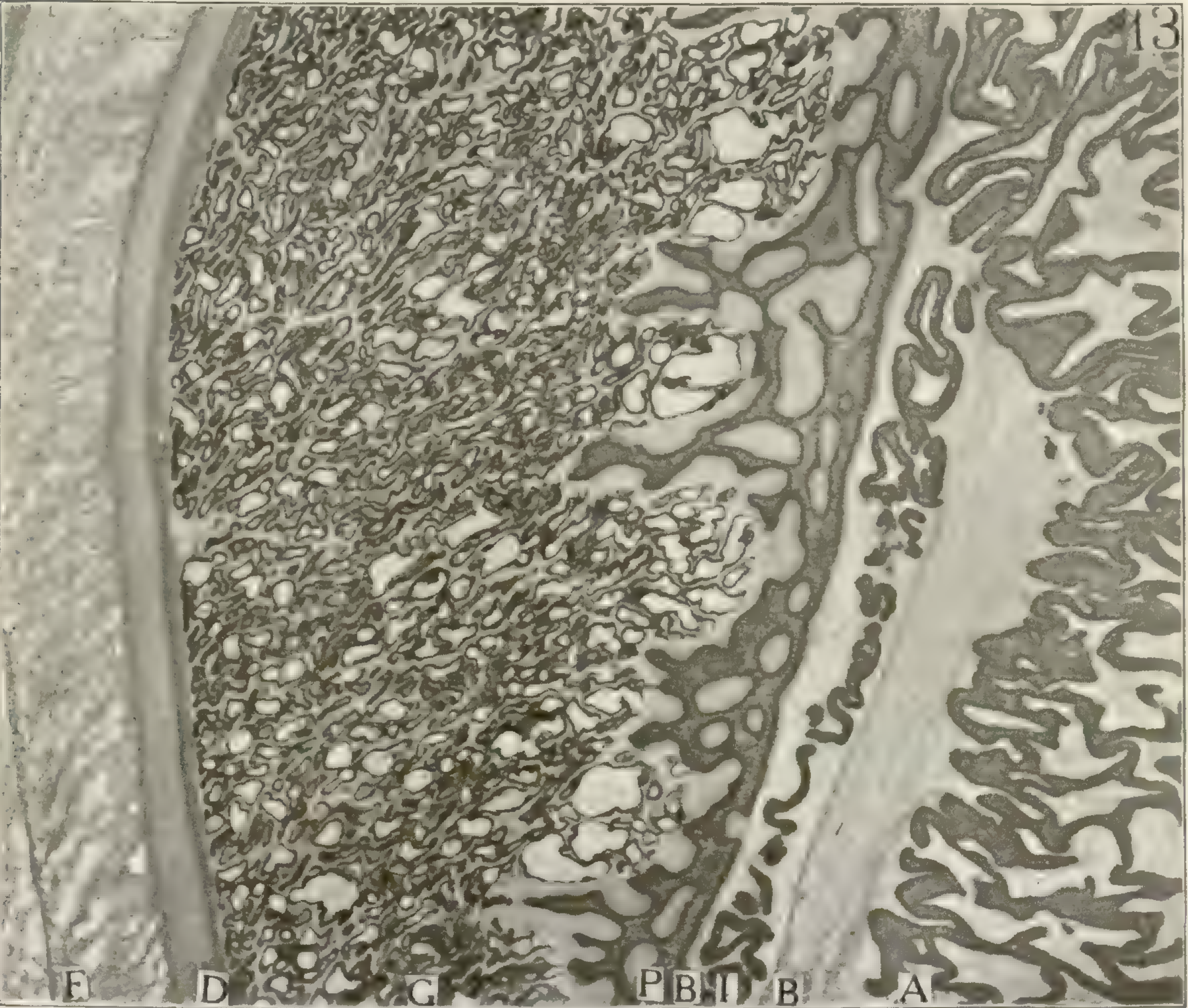
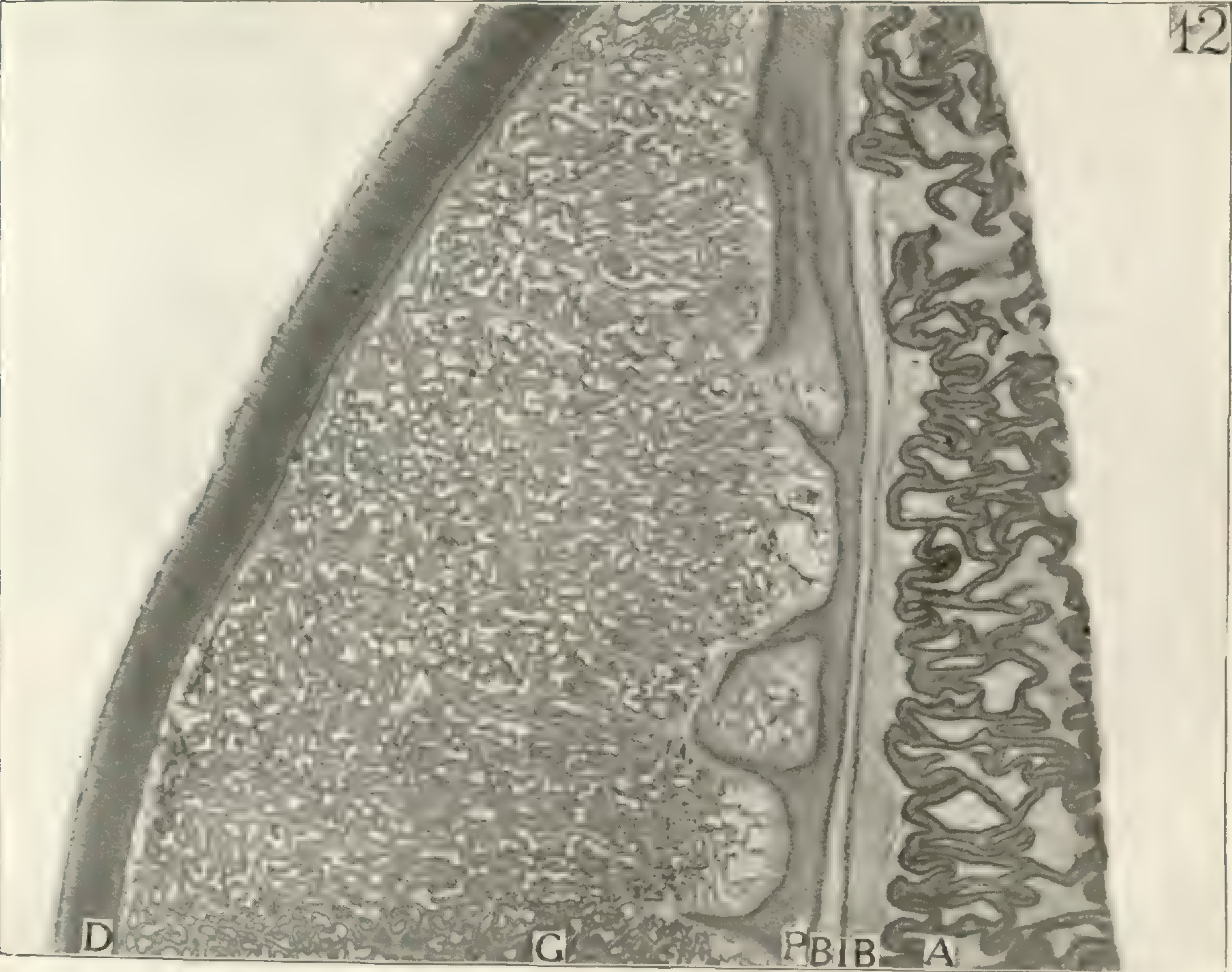
ATKINSON on DICTYOPHORA AND ITHYPHALLUS



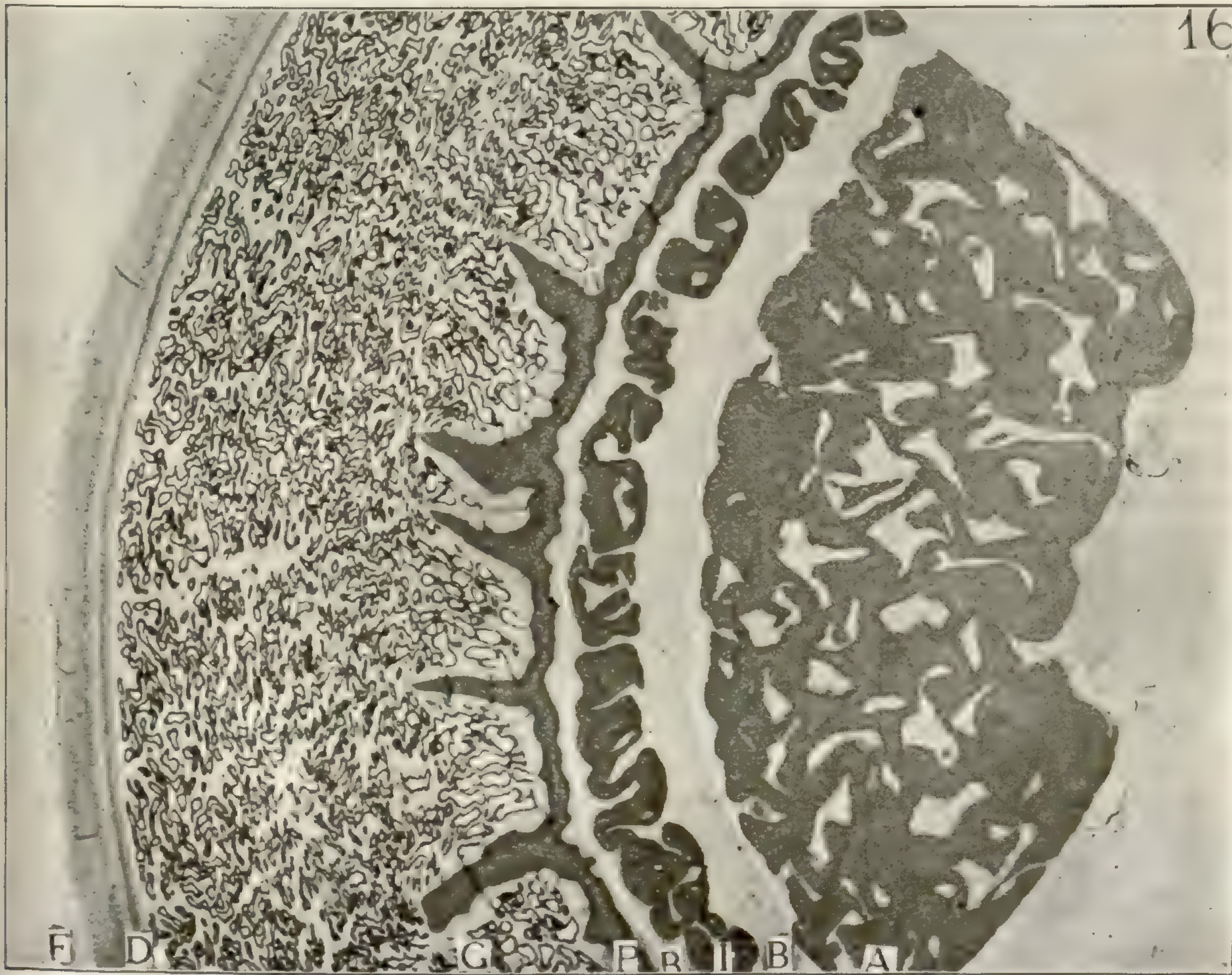
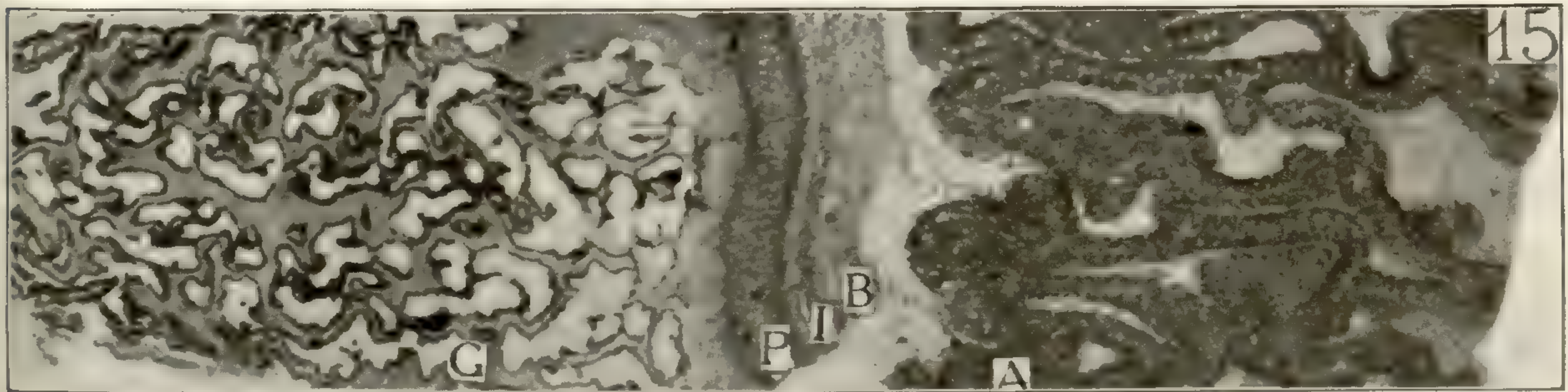
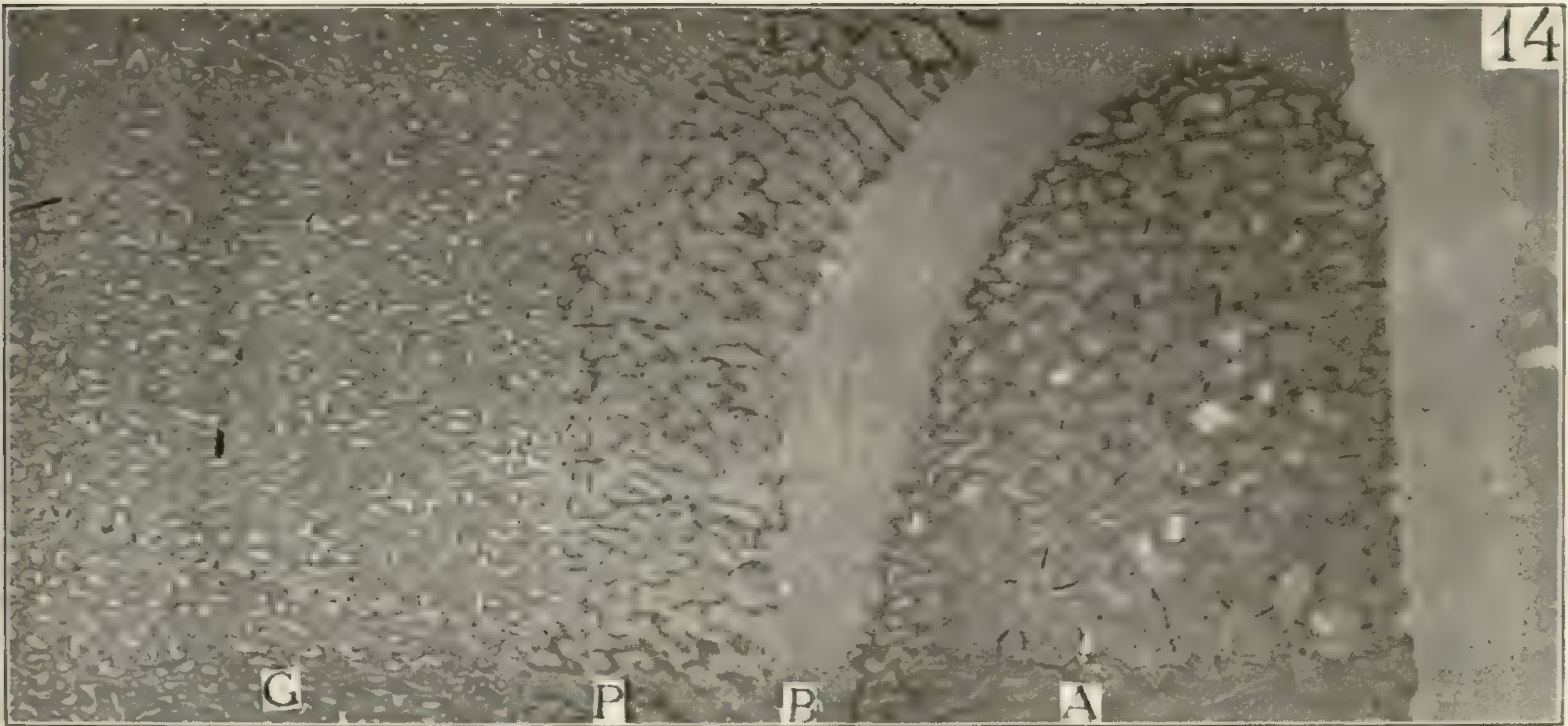
ATKINSON on DICTYOPHORA AND ITHYPHALLUS

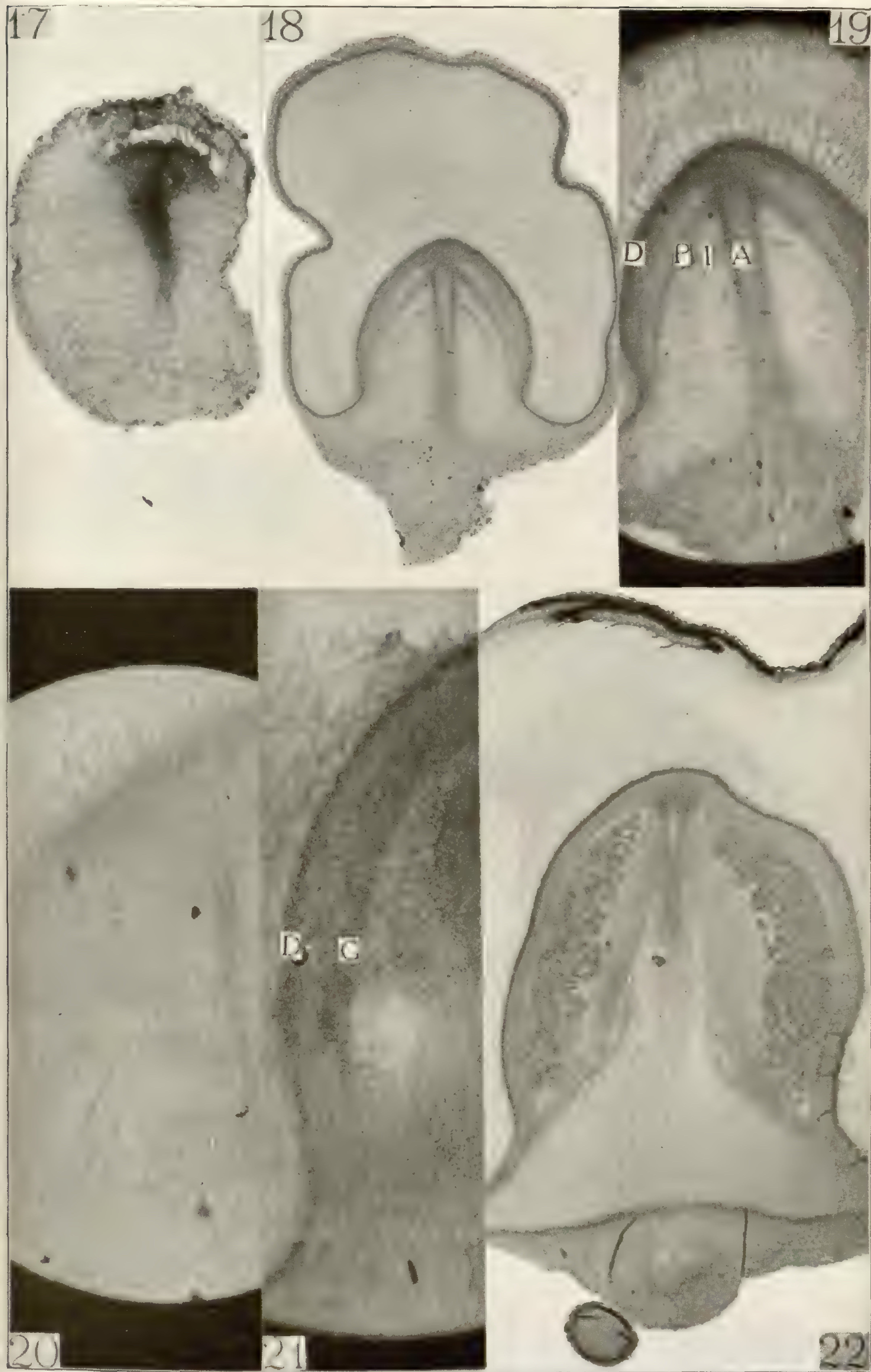






ATKINSON on DICTYOPHORA AND ITHYPHALLUS





ATKINSON on DICTYOPHORA AND ITHYPHALLUS

THE AFFINITIES OF GEINITZIA GRACILLIMA¹

EDWARD C. JEFFREY

(WITH PLATE VIII)

In a recently published memoir in collaboration with Dr. ARTHUR HOLLICK, the writer has shown that there is good anatomical evidence for regarding numerous mesozoic conifers, which have in the past, from a consideration of their external habit alone, been considered to belong to the Taxodineae or Cupressineae, as in reality appertaining to the araucarian tribe of the Coniferales. In the memoir in question,² disjoined leafy twigs and more or less fragmentary relics of cones were described anatomically. In the case of the vegetative twigs it was shown that the anatomical structure was entirely araucarian, and similar evidence was somewhat less conclusively given in the case of the cones. Unfortunately, it was not possible in any of the Kreischerville material to investigate the woody axis of a cone, which would obviously furnish the clearest evidence as to the true affinities of the reproductive branches of the Kreischerville material. The cone scales alone, although furnishing in the opinion of the present writer ample evidence of their araucarian relationships, might by those less experienced in the details of coniferous anatomy still be considered as belonging to strobili of the Taxodineae or Cupressineae. Happily another cretaceous deposit has finally furnished the much to be desired testimony, which apparently puts beyond all possible question the araucarian affinities of the cretaceous remains, which have in the past been referred by purely systematic paleobotanists to the living genus *Sequoia*.

The material on which the present article is based was derived from the Matawan Formation, which clearly overlies the Raritan or Upper Potomac beds from which the Kreischerville material

¹ Contributions from the Phanerogamic Laboratories of Harvard University, no. 31.

² HOLLICK, ARTHUR, and JEFFREY, E. C., Studies of cretaceous coniferous remains from Kreischerville, New York. Mem. N.Y. Bot. Gard., no. III. May 1909.

was obtained. Various writers have recorded the abundance of cones of *Sequoia gracillima* in the clays of the coastal bluffs of Cliffwood, New Jersey.³ Through the kindness of Dr. HOLLICK and particularly of Mr. E. W. BERRY of the Geological Department of Johns Hopkins University, the present writer has received from time to time numerous specimens of this species. Unfortunately all of these were either too thoroughly impregnated with iron pyrites or in too bad a condition of preservation to yield any satisfactory evidence when examined microscopically. After repeated personal visits to the Cliffwood bluffs, the writer was at last rewarded in the spring of 1909 by the discovery of a single cone in which the axis was in a good condition of preservation. The figures in the present article, with the exception of the first, are made from the preparations of this cone.

Fig. 1 shows the surface of a pyritized cone of *Sequoia gracillima*, so-called, from the two opposite flattened surfaces. In *a* is shown the best preserved surface of the cone, while in *b* the hexagonal outlines of the cone scales, and often their surface as well, are obscured by incrustations of the iron pyrites, which infiltrate the substance of the cone itself. In cones showing a better condition of preservation than is generally found in the Cliffwood material, the center of the peltate scales is marked by a profound depression.

Fig. 2 reproduces a transverse section of the peduncle of the well preserved specimen described above. Higher up, the axis of the cone is not so well preserved, being somewhat flattened and considerably more impregnated with granules of iron pyrites. The peduncular portion, however, is in an admirable condition of preservation, even the soft tissues of the phloem and the cortex being clearly recognizable. The pith, which appears in the center of the figure, is characterized by the presence of the same sclerotic nests, composed of stone cells, described in the memoir of Dr. HOLLICK and the present writer, cited above, for the vegetative twigs of a number of conifers which are now known to be of araucarian affinities on the basis of their microscopic structure. Outside

³ NEWBERRY, J. S., Flora of the Amboy clays. *pl. 9. figs. 1-3.* 1896; BERRY, E. W., Flora of the Matawan Formation. *Bull. N.Y. Bot. Gard.* 3:no. 9. 1903; BERRY, E. W., Additions to the flora of the Matawan Formation. *Bull. Torr. Bot. Club* 31:Feb. 1904.

the pith is the well developed woody cylinder, which is succeeded by a zone of well preserved phloem of about a third its diameter. External to the phloem lies an irregular and partly destroyed cincture, representing the cortex. The magnification is not sufficient to show that in the cortex there are sclerotic cells similar to those found in the pith.

Fig. 3 shows the structure of the higher part of the cone as seen in longitudinal section. Centrally lies the medullary tissue, largely occupied by stone cells. Near the region of the wood the sclerotic aggregations give place to thin-walled parenchymatous elements. The wood is crossed on the right side of the figure, which shows it in a good condition of preservation, by shallow medullary rays from one to three or four cells in height. The rays, as seen in the transverse and the longitudinal radial sections, are uniseriate. The broad, so-called fusiform, rays found in the pinelike *Abietineae* are entirely absent. Part of the phloem adheres to the surface of the wood on the right, while on the left both phloem and cortex are absent.

Fig. 4 shows a detailed longitudinal section of part of the pith. The stone cells, with their layered and laminated walls, can be seen intermingled with the thin parenchymatous elements, which constitute the rest of the medullary tissues. The lamination of the walls of the stone cells is to be regarded as the result of the conditions of fossilization, as these cells in similar material from the Kreischerville deposits, in the best preserved twigs, show no indication of lamination.

Fig. 5 shows a transverse section of part of the lower region of the cone axis. The phloem and xylem are both present and in a good condition of preservation. The former occupies the upper part of the figure and is obviously not of the type found in the *Cupressineae* and *Taxodineae* (*Sequoiineae*), since the striking alternating stripes of hard bast fibers, which are characteristic of the phloem of the two coniferous tribes just mentioned, cannot be seen. A zone of decay marks the position of the cambium. Below this region appears the wood, composed of rather small tracheids. The rays can scarcely be made out, since they are composed of smooth thin-walled cells, which very readily collapse.

In the wood on the extreme right and left and radially nearer the right center, are seen dark patches, which on superficial examination might appear to be the resin cells, characteristic of the wood of the Cupressineae and Taxodineae. An attentive microscopic examination of these, however, shows them to be clusters of black crystals of iron pyrites contained in the tracheids of the wood.

Fig. 6 illustrates the structures of the wood as seen in longitudinal section. Toward the left can be seen the cells of the pith, while to the right of these can be made out the ringed and spiral elements of the primary wood. Further to the right, and occupying over half of the field, is part of the secondary wood. The elements of the wood are narrow and are occupied by pits which in no case are contiguous or in more than a single row. With the restricted conception of araucarian woods which has prevailed almost until the present time, pitting of this character would not be regarded as indicative of araucarian affinities. As the result of recent investigations into the structure of mesozoic conifers, we now know that the wood genus *Araucarioxylon* Kraus does not cover all the araucarian ligneous types of the past. This genus is characterized by alternating or flattened pits on the radial walls of the tracheids, by smooth-walled ray cells, and incidentally by the absence of resin canals formed as a result of wounding. As has been pointed out by the present author in the memoir on the Kreischerville conifers and in other publications there cited, there are two other araucarian wood types in the Mesozoic, namely *Brachyoxylon* and *Araucariopitys*. In the former the pits are often of the flattened or alternating character found in the *Araucarioxylon* type, but likewise are as often neither alternating nor flattened. Further, *Brachyoxylon* differs from *Araucarioxylon* in the formation of resin canals as the result of wounding, and resembles it in the possession of smooth-walled ray cells. Writers on cretaceous plants in general have failed to distinguish *Brachyoxylon* from the *Araucarioxylon* type. In *Araucariopitys* we find, in addition to the pitting and wound reactions of *Brachyoxylon*, the strongly pitted ray cells which are characteristic of the Abietineae. This enumeration of araucarian woods, however, is not

exhaustive, for recently a new type has been described⁴ in which the alternating or flattened pitting, which on the former understanding of the Araucarineae was characteristic of the wood of this coniferous stock, is entirely absent. Thus we come to the paradox of an araucarian wood without araucarian pitting. Quite recently Miss GERRY has shown⁵ that the essence of the araucarian ligneous type is the absence of the bars of Sanio in the tracheids, and not necessarily the mode of arrangement or the shape of the radial pits of the tracheids.

With the citation of recent investigations on coniferous woods, we are now in the position to consider the affinities of our cone axis. It has been pointed out in the foregoing paragraph that the cone under consideration had tracheids with unapproximated, unflattened, and non-alternating pits. Under the former conceptions as to the affinities of coniferous woods, our axis would certainly have been placed with *Cedroxylon* or even *Cupressinoxylon*, rather than with the Araucarineae. The smooth walls of the ray cells exclude our axis from the ligneous genus *Cedroxylon*, which properly conceived is characterized by the strongly pitted character of the medullary ray parenchyma, as has recently been insisted upon by GOTHAN. The wood of the cone axis under discussion is, as has been indicated above, in parts in an admirable condition of preservation, and it has been accordingly possible to ascertain definitely that the bars of Sanio are quite absent. This important criterion brings our wood under the Araucarineae in the broadest sense, and among the numerous ligneous types which are now known to have belonged in this formerly very varied and comprehensive coniferous tribe. Among the known types of araucarian woods, it obviously falls into the genus *Paracedroxylon* of SINNOTT.

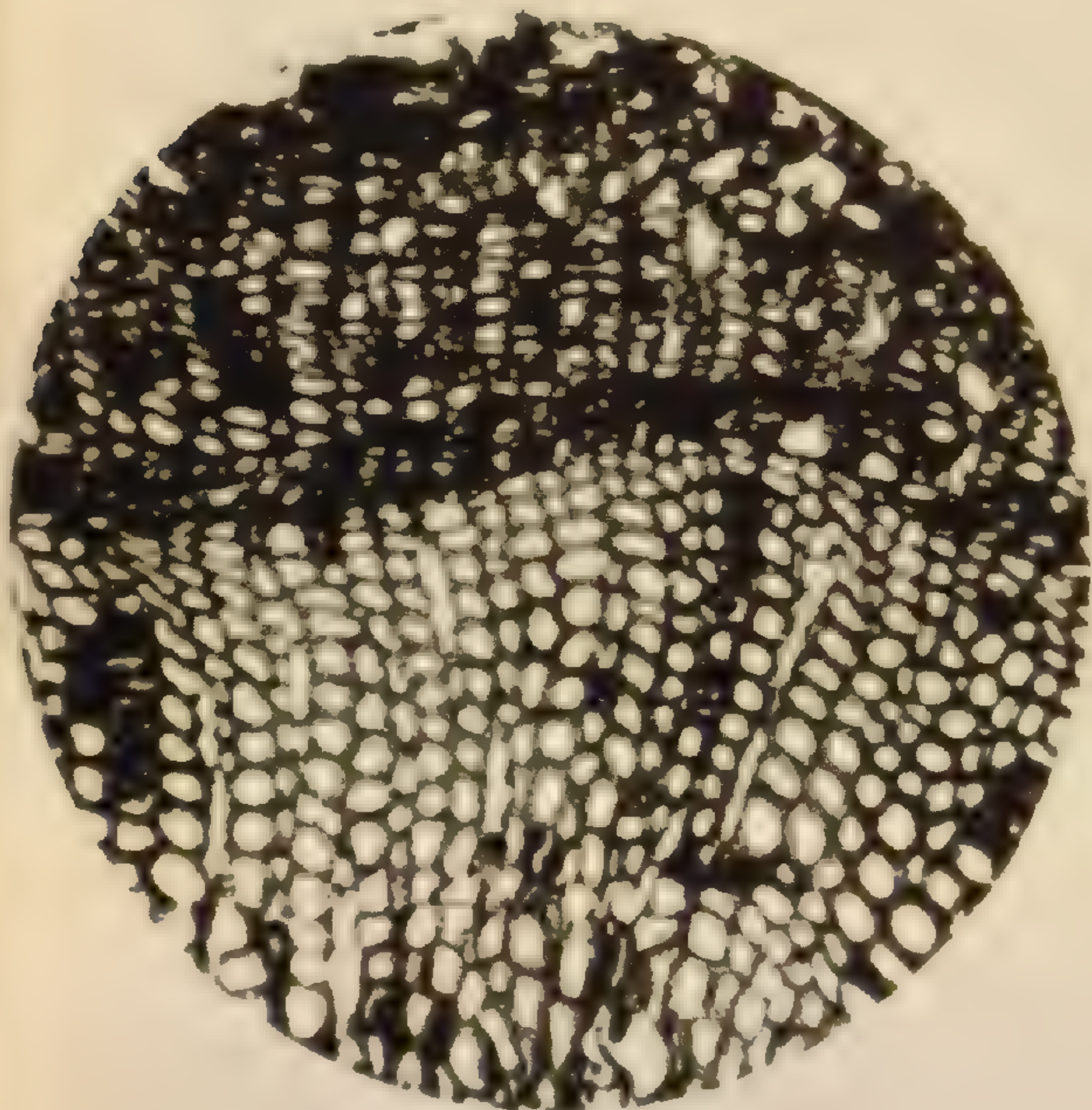
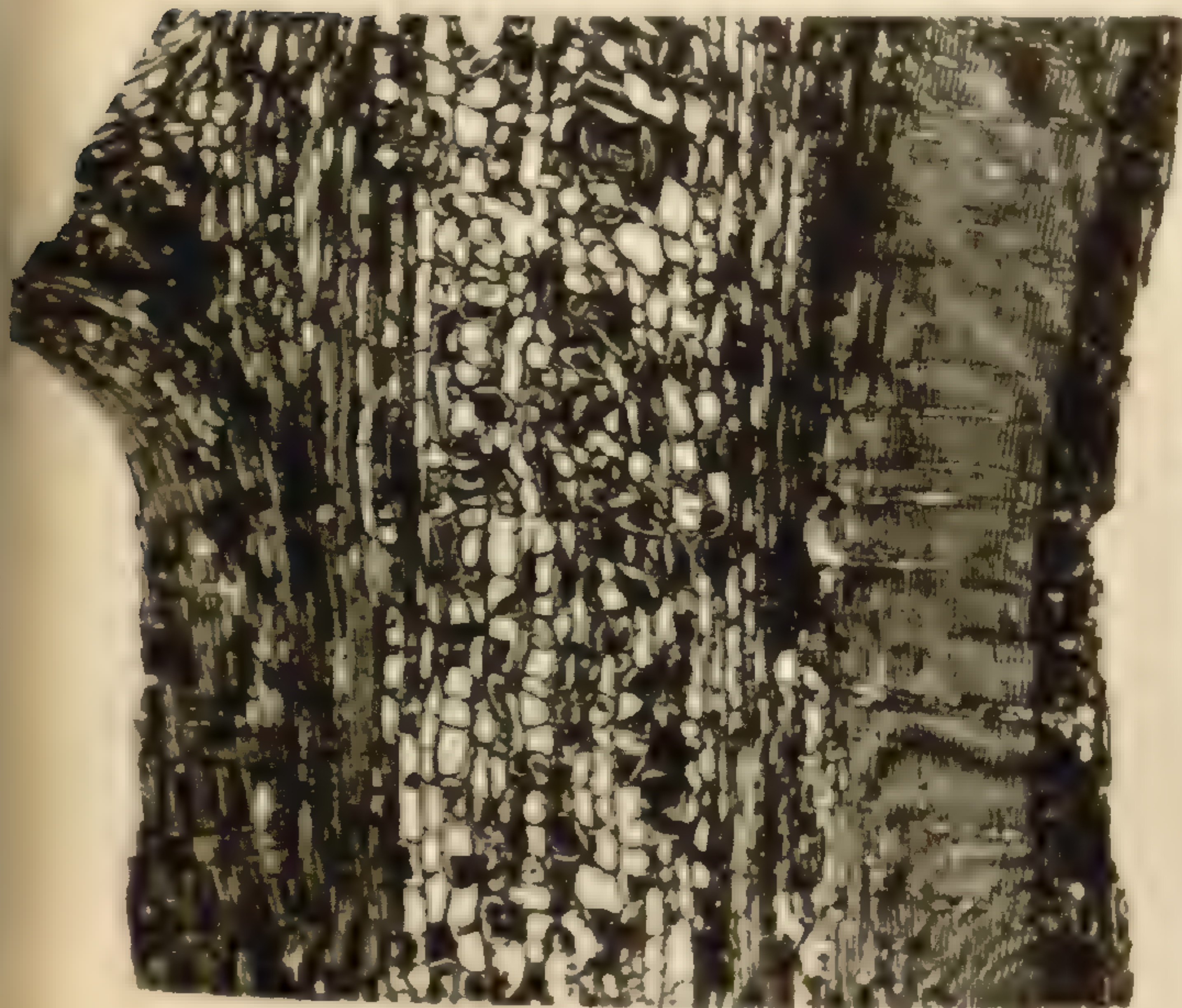
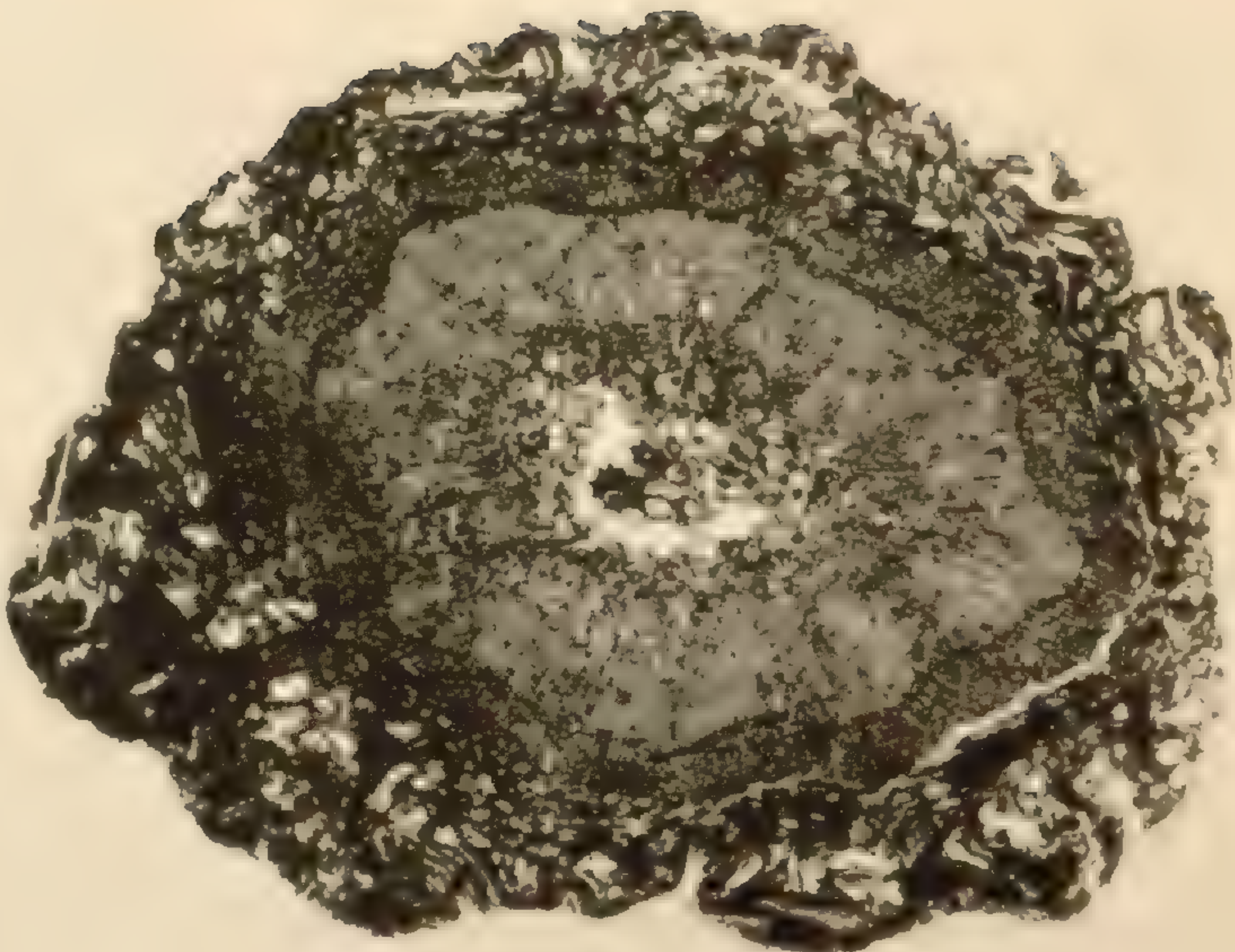
Conclusions

It is apparent from the description of the cone axis of the supposed species of *Sequoia* known as *S. gracillima*, given in the fore-

⁴ SINNOT, E. W., *Paracedroxylon*, a new type of araucarian wood. *Rhodora* 11:165-173. 1909.

⁵ GERRY, ELOISE, The distribution of the "bars of Sanio" in the Coniferales. *Annals of Botany* 24:119-124. 1910.

going paragraphs, that our specimen cannot belong in any way to the genus as at present anatomically characterized. For in the very important particulars of wood structure, organization of the phloem, as well as the constitution of the pith and cortex, it differs absolutely from all existing members of the Cupressineae and Taxodineae. It is equally clear, from a consideration of all the features of histological structure just indicated, that the cone axis under discussion belongs with those Araucarineae of the more primitive type which became extinct with the close of the Mesozoic period. There remains, however, one point to be elucidated. It has been shown in the memoir on the conifers of Kreischerville, frequently cited above, that the vegetative twigs known as *Sequoia Reichenbachii* had structure of the *Brachyoxylon* type, that is, a type intermediate between the true *Araucarioxylon* type and the *Paracedroxylon* type described by SINNOTT. Our cone, which beyond any reasonable question belongs in the same genus, has not the *Brachyoxylon* type of wood, but on the contrary shows all the features of ligneous organization found in *Paracedroxylon*. It is a somewhat well established principle in coniferous anatomy at the present time, which is applicable to an even wider range of anatomical facts, that the reproductive axes of this order of gymnosperms are apt to perpetuate the structure of ancestral types. For example, the structure of the wood in the *cones* of existing pines is now known to retain the type of wood structure found in the *vegetative* branches of the pines of the Lower Cretaceous. Applying this principle to the cone axis at present under consideration, it is rendered probable that the *Paracedroxylon* type was characteristic of araucarian vegetative twigs representing the ancestral forms from which the so-called cretaceous sequoias were derived. We have thus another and independent argument for the thesis maintained for some years by the present author, in opposition to the received view of most other writers on the conifers, namely, that the Araucarineae characterized by the *Araucarioxylon* type of wood cannot be regarded as primitive members of the stock, but that the *Brachyoxylon*, *Araucariopitys*, and *Paracedroxylon* araucarian types are all older than *Araucarioxylon* and connect it in one way or another with the type of wood found in the



Abietineae, particularly the older Abietineae, of the *Pinus* type. The discovery of an ancient pinelike conifer, *Prepinus* Jeffrey, with generalized short shoots bearing many spirally arranged leaves, characterized by the possession of fibrovascular bundles with well developed centripetal wood of the archigymnospermous type, as well as the details of organization found in the leaves of certain *Cordaite*s, appears to make it quite clear that we must look in the direction of the Abietineae, rather than in that of the Araucarineae, for the primitive representatives of the Coniferales.

Summary

1. *Sequoia gracillima*, so-called, cannot be regarded as belonging to the living genus to which, on its superficial characters, it has been referred.

2. It is an araucarian conifer, and in accordance with accepted principles of nomenclature should in future be referred to the genus *Geinitzia*.

3. The structure of the cone axis in the so-called *Sequoia gracillima* (*Geinitzia gracillima*) vouches for the accuracy of the reference of detached cone scales of species of *Geinitzia*, and other araucarian conifers of similar type from the Lower Cretaceous, to araucarian affinities.

4. The structure of the cone axis of *Geinitzia gracillima*, being less like the *Araucarioxylon* type than that found in the vegetative twigs of representatives of the genus from the Lower Cretaceous, furnished additional and independent evidence for the derivation of the araucarian stock from an ancestry essentially resembling the existing Abietineae.

HARVARD UNIVERSITY

EXPLANATION OF PLATE VIII

FIG. 1.—A cone of *Geinitzia gracillima*, slightly reduced, viewed from opposite sides.

FIG. 2.—Transverse section of the peduncle of the cone of *G. gracillima*. $\times 40$.

FIG. 3.—Longitudinal section through a higher region of the same cone. $\times 40$.

FIG. 4.—Longitudinal section through the pith of the same. $\times 80$.

FIG. 5.—Transverse section of the lower region of the cone axis. $\times 180$.

FIG. 6.—Longitudinal radial section of the wood of the cone. $\times 180$.

STUDIES ON THE RELATION OF THE LIVING CELLS TO TRANSPIRATION AND SAP-FLOW IN CYPERUS. I

JAMES BERTRAM OVERTON

(WITH ONE FIGURE)

Historical discussion

Recent studies have revived with considerable vigor the doctrine that the presence of the living cells in the stem is necessary for the ascent of sap. The earlier evidence as to the necessity of living cells for sap-flow, as presented by GODLEWSKI (15) and supported by WESTERMAIER (41, 42) and JANSE (16), was shown to be inadequate by STRASBURGER (30, 31) in a series of elaborate experiments, in which long portions of stems were killed with steam, hot water, and poisons, and the dead parts proved to be still capable of conduction. Several authors have refused to accept STRASBURGER'S conclusions and have presented important criticisms of his experimental work.

The vitalistic theory of sap-flow, as it may perhaps be called, has been vigorously exploited by URSPRUNG (32-37) and further supported by his student ROSHARDT (24). URSPRUNG'S methods and conclusions, however, have in turn been severely criticized by JOST (17, 18), DIXON (9-12), and CZAPEK (7, 8).

URSPRUNG conceives that the living cells of the stem either may function in keeping the vessels in a proper state for conduction, or else they may take a direct part in the elevation of the sap. He believes that their lifting power is the more important function in tall plants, but that in low herbaceous ones the living cells may keep the vessels in a proper condition for conductivity. In support of his views he has carried out a series of experiments, in which portions of the petioles or stems of rooted plants were killed with heat, low temperature, or poisons.

URSPRUNG'S (32) experiments were carried out on leaves of *Primula obconica*, *Pelargonium zonale*, *Begonia* sp., *Impatiens* sp.,

and on stems of *Vicia Faba*, *Phaseolus multiflorus*, *Hedera Helix*, and *Fagus silvatica*. By treating short stretches (1, 2, or 3 cm.) of the petioles of *Primula* with steam for 3 minutes, he found that no immediate, visible effect is produced on the leaves; while if longer portions (6–9.5 cm.) are killed, wilting follows in about 4 hours. These observations are further supported by similar experiments on *Pelargonium*, *Begonia*, and *Impatiens*, from which he finds that the leaves wither more and more rapidly as the lengths of the killed portion are increased, even when the killed region is protected, and this shows, according to URSPRUNG, that wilting is not due to a lateral evaporation in the killed portion, but to a lack of sufficient water supply. He finds no stoppage of the vessels as the result of treatment. If stoppage of the vessels were caused by the treatment, he believes the leaves would wither as quickly above a short as a longer killed region.

For the study of sap-flow in stems URSPRUNG chose three plants of *Phaseolus* as nearly alike as possible. Removing all except the two topmost leaves, he killed the stems of two plants for 40 cm. above the soil, leaving 20 cm. untreated below the leaves of one plant. The killed portion was left exposed, while the other was covered with paraffin. The leaves on both plants wilted in 2–4 days, being entirely dry in 4 days. The leaves of the unprotected plants wilted faster. A plant 63 cm. high was killed for 22 cm. above the soil; the leaves remained turgescient for 19 days. From these and other experiments on *Phaseolus* he concludes that the longer the killed portion of the stem, the sooner the leaves above wither, and that the living cells are necessary to the elevation of water in sufficient quantities. On killing 80 cm. of a rooted stem of *Hedera*, the youngest leaves were observed to wilt in 1.5 days. Leaves situated below the killed region were not affected. Histological examination failed to reveal any stoppage of the vessels. In case of the stem, withering in *Fagus* could be observed in 2 days when 80 cm. of the stem were killed, while the leaves remain turgescient for 20 days when only 3 cm. were killed. In repeating some of his experiments on *Fagus*, he (34) observed that wilting and discoloration in spots occurred on the leaves. Similar discoloration was also observed when leaves were simply deprived

of water. In the case of leaves which bore spots, he observed that they still remained after drying, and concluded that they were not caused by the heating of the stem. By heating only the outer portions of a "tolerably thick" *Fagus* stem with steam for "a short time," he found that the leaves remained turgid for 9 days, and assumes that the plant can conduct water if only some of the living cells are present. In the case of several other experiments on woody stems, portions of which have been killed with steam, he found that the vessels were stopped for several centimeters above the killed portion. The wilting supervened in these cases no sooner than in other cases in which no stoppage was observed. He believes that wilting may occur in cases when stoppage is not present.

URSPRUNG (34-37), parallel with steam, has also employed girdling experiments on about 20 species of plants besides *Fagus*. When 10 cm. of richly leaved branches of *Ulmus* and *Populus* are killed with steam, the leaves wilt in 1-2 days, while in *Prunus* they last for 25 days under similar treatment. He has also killed branches and stems for a length of 3-10 cm. near the top and near the base. The nearer the killed stretch is to the leaves, the sooner they wither. With the exception of *Prunus*, the leaves remain longer turgescient, some ten times as long, when 3 cm. than when 80 cm. are killed. His girdling experiments gave very divergent results in the different plants studied. *Viburnum* kept its leaves turgescient for 45 days; *Ulmus* leaves began to wilt in 1 day. URSPRUNG concludes from these heating and girdling experiments that two factors are concerned in the death of the leaves: (1) increased resistance to sap-flow, (2) diminution of the power of transportation. He believes that the very great difference in time of wilting in different plants is due not to differences in their sensitiveness, but to a difference in their capacity to conduct and hold water under the condition of the experiment. A slow water transport may be due to an increased resistance to flow or to a decrease in the power of the transportation of the stem. Since stoppage of the vessels is not universally present in treated stems, he thinks that the increased resistance to flow is not to be considered. According to him the transport of water is partly

physical and partly vital, and the vital factor is eliminated by killing a portion of the stem.

URSPRUNG (34) has also used ether, induction currents, and low temperature to kill portions of the stems of both cut and rooted plants. By removing half of the cortex for 10 cm. from the branches of *Fagus* and exposing the wound to ether, the leaves were observed to wither in 2-3 days. By cooling portions of the branches of the same species with ice for 12-30 cm., the leaves above were always observed to wilt in 2-6 days, depending on the length of the cooled portion. All of these researches cause URSPRUNG to conclude that the living cells are in some way essential to the ascent of water.

STRASBURGER also performed some experiments on plants in connection with the roots, killing various stretches of the stem with heat. URSPRUNG (32, 33) in discussing these experiments notes that the leaves above fade, and concludes that the water does not pass through the killed portion in sufficient quantities to supply the leaves. He thinks, therefore, that STRASBURGER'S experiments show that the living cells of the stem are necessary in order that a sufficient amount of water may ascend to supply the leaves. He further cites in favor of his own view the experiments of BOEHM (3), in which 18 cm. of stems of bean plants were killed with steam, noting that the leaves above "lived" for a period not longer than 3 weeks; wilting usually occurred sooner. BOEHM considered that the wilting was due to a plugging of the vessels with mucilage or to a severing of the water columns. URSPRUNG passes over this observation with the remark that it teaches nothing new.

Considering the possibility of the participation of the living cells of the stem of a plant in sap-flow, DIXON (9) has repeated some of the experiments of URSPRUNG (32) with rooted stems and attached leaves. Although he fully supports URSPRUNG'S account, he gives quite a different interpretation of the results obtained. When only "short lengths" of the stems of *Primula*, *Chrysanthemum*, *Syringa*, *Philadelphus*, and *Cytisus* were killed by heat, the leaves beyond "scarcely suffered," little injury appearing; but when 2-5 cm. lengths were killed, the leaves showed injury in proportion as the length of the killed region was increased.

This progressive effect DIXON attributes to the probable introduction into the leaves of poisonous or plasmolyzing substances from the dead cells. Three branches of *Syringa* were placed in water and three others in a filtered decoction made by boiling stems of the same kind and filtering and cooling the fluid. The stems which stood in the decoction wilted its leaves in 2 days, while the stems in fresh water wilted their leaves in 5 days. As compared with stems set in fresh water, wilting took place much faster in those placed in the decoction. In order to show that this effect was not due to a clogging of the vessels, the immersed ends of the stems were frequently cut away. The injurious properties of the decoction remained, showing that wilting was probably not due to a clogging of the vessels by comparatively impermeable substances, since these would have been removed by the repeated filterings. DIXON suggests that it is possible that the application of heat in these experiments may to some degree have permanently interrupted the water supply by breaking the water columns.

URSPRUNG (35-37) has repeated DIXON's experiments described above, using *Impatiens sultani*, and has reached the same results. Microscopical examination showed him that the vessels at the base of the stem were plugged with a brown mass. Upon bringing a plant which had stood in a decoction into a moist room, the leaves again became turgescient. When stems which had become stopped by standing in a decoction were placed in water, the leaves rapidly became turgid. The leaves of plants which had been standing in a solution of CuCl_2 remained wilted when brought into a moist room. He was unable to find stoppage in plants which had been placed in CuCl_2 . He concludes, therefore, that his researches show that the wilting of the leaves is not due to a poisonous action of the decoction, but to the insufficient water supply caused by the stoppage of the vessels. He further placed a rooted *Impatiens* plant in a concentrated *Impatiens* decoction. After 2 days, microscopical examination showed that the protoplasm of the root hairs was in a perfectly normal condition. The leaves of this plant remained completely turgescient, while those of a cut shoot placed in a decoction rapidly wilted. The decoction possesses, therefore, according to him, no plasmolyzing substances.

DIXON (10-12) finds that water forced through a steamed portion of a stem is tinged with a brown substance, while water forced through an unsteamed or otherwise heated stem emerges as a clear liquid. He also performed experiments on cut branches of *Syringa*, placing some in water and others in a decoction of the same plant. The leaves on the stems set in water wilted in 5 days; those set in the decoction wilted in 3 days. URSPRUNG, performing similar experiments with *Impatiens* and obtaining similar results, does not believe that the leaves fade because they are poisoned by the decoction, but that they fade because of a stoppage of the vessels at the cut end of the branch with a brown mass which interferes with the water supply. Among other experiments along this line, DIXON killed one arm of a bifurcated *Syringa* shoot with hot water. The leaves were then removed and pure water was supplied through it to the living branch, so that the leaves on it received their water supply through the main stem and through the dead branch. In spite of the ability of the leaves on the living branch to receive their water supply from the roots as well as through the dead branch, they soon showed signs of wilting, resembling the early stages of fading characteristic of the leaves above a heated portion. DIXON thinks that the leaves fade because substances are formed during the heating of the stem which are carried to the leaves and act injuriously upon them. He further concludes from his experimental evidence that the fading of the leaves on a heated stem is not the same as occurs normally when leaves are simply deprived of water. In leaves above a killed stretch he observed a contraction of the protoplasts of the mesophyll cells and a discoloration of the chloroplasts in the areas which were turning color. DIXON holds, therefore, with VESQUE (38, 39) that in one case the leaves die because they dry, while in the other case they dry because they die, which appears from my observations to be a true statement of the facts.

ROSHARDT (24), proposing to study the problem of sap-flow as outlined by URSPRUNG, has performed experiments on 131 species of 59 families of shrubs and herbaceous seed plants, by killing certain stretches of the petioles, stems, and branches with steam, ether, xylol, or low temperature, and determining what effect the

treatment may have on sap-flow. For comparison with my observations on *Cyperus*, ROSHARDT's experiments on the grasses are of particular interest. Experiments were made upon *Bromus sterilis*, *Bromus hordeaceus*, *Dactylis glomerata*, *Poa pratensis*, *Agropyrum repens*, *Glyceria plicata*, *Arrhenatherum elatius*, *Lolium perenne*, *Cynosurus cristatus*, *Secale cereale*, *Miscanthus polydactylos*, and *Bambusa aurea*. With the exception of *Secale*, *Miscanthus*, and *Bambusa*, 5-10 similar halms were killed for the same stretch. Although the grasses agree generally in the morphological structure, he finds that their response to the treatment was widely different. He was unable to observe distinct wilting of the leaves except in *Bromus hordeaceus*, and then only in direct sunlight. In other species of the grasses, yellow-red spotting together with a yellow discoloration of the leaves appeared, which was followed by shriveling. The leaves began to dry first at the tips and fading began from below upward, the upper leaves drying last. The flowers and fruits remained fresh longer than the leaves, and the halms dried last. The leaves of *Miscanthus* wilted from above downward on the stem. The lack of water was often indicated by a rolling of the leaves, which occurred in *Agropyrum* and *Bambusa*. He tabulates the results in cases in which a length of 10 cm. of the halms was killed in order of their drying: *Bromus sterilis* (dry in 17 days), *B. hordeaceus* (16 days), *Bambusa* (13 days), *Dactylis* (12-14 days), *Glyceria* (10 days), *Poa* (9 days), *Lolium* (9 days), *Arrhenatherum* (about 8 days), *Miscanthus* (7 days), and *Secale* (about 7 days). When 20 cm. of the halms are killed, the following order results: *Agropyrum* (12-13 days), *Bromus hordeaceus* (12 days), *Bambusa* (10 days), *Glyceria* (8 days), *Poa* (5-7 days), and *Miscanthus* (2-5 days when 22 cm. were killed). It will be seen that the leaves of *Bromus hordeaceus* remain fresh 16 days when 10 cm. are killed, while its leaves dry more quickly (12 days) when 20 cm. are killed. He feels justified in concluding from these results that the longer the killed stretch the sooner the leaves above indicate a deficiency in the water supply by drying.

ROSHARDT's tables show that killing the same stretch of the stem of nearly related forms of the same genus produces very different effects in the time of wilting of the leaves. He has compared

several plants as to time of wilting when 10 cm. of the stem were treated, with the following results: *Hypericum* 17 cm. (22 days), *Lycium* 20 cm. (16-17 days), *Physalis* 20 cm. (9 days), *Anthriscus* 16-20 cm. (about 10 days), *Pisum* 27 cm. (9 days), *Hemerocallis* 20 cm. (9 days), *Sambucus* 20 cm. (about 9 days), *Rheum* 12 cm. (12 days), *Bromus sterilis* 10 cm. (12 days), *Spiraea Thunbergii* 13 cm. (11 days), *Ampelopsis* 8 cm. (12-13 days). The leaves of the following plants withered very quickly when 10 cm. of the stems were killed: *Polygonum virginianum* 2.5 cm. (0 days), *Circaea lutetiana* 2.5-3 cm. (0 days), *Ficaria* 9.5 cm. (0 days), *Primula obconica* 10 cm. (0 days), *Malva* (petiole) 10 cm. (0.5 day), *Urtica* (petiole) 2 cm. (about 1 day), *Campanula rapunculoides* 2 cm. (1 day), *Petunia* 2 cm. (1 day), *Crepis* (young plant) 5 cm. (1 day), *Narcissus Pseudo-Narcissus* 6 cm. (1 day), *Gentiana lutea* 9 cm. (1 day), *Adenostyles* 10 cm. (1 day), *Verbena* 13 cm. (1 day), *Cannabis* 8 cm. (about 1 day), *Helianthus* (young leaves) 3.5-6 cm. (1-2 days), *Primula elatior* 2-7 cm. (1-1.5 days).

Besides using steam and low temperature to kill various stretches of the stems and petioles, ROSHARDT has employed ether and xylol, applying the fluid to the parts with a fine brush. The petioles of 8 plants of *Arum maculatum* were treated with ether, and those of 12 other plants with xylol for a distance of 7-14 cm. He found that the leaves wilt, discolor, and dry in 9-14 days. By treating a 23 cm. stem of *Phaseolus multiflorus* with xylol for a 10 cm. stretch, the leaves were observed to wilt in 2 days and to be dry in 4 days. The leaves of *Tropaeolum*, whose petioles were painted with xylol for 6-20 cm., wilted in 2-4 days and dried in 4-7 days; controls cut and placed in the neighborhood wilted in 2 days and dried in 7 days. He carried out experiments on *Oxalis Acetosella*, observing what effect the painting of the petioles with ether or xylol would have on the sleep movements of the leaves. A number of petioles of 12 plants were painted with ether for "short stretches." Immediately the leaves assumed the characteristic sleep positions, which they kept until evening; they had assumed their normal positions by the next morning; after 4 days, discoloration and wilting took place. A control plant was stroked with a brush without the ether and the leaves behaved normally. Por-

tions of the petioles of 4 plants of *Oxalis* were painted with xylol for 3 cm.; the plants failed to assume the sleep position; the leaves wilted in 2 days and dried in 3 days. Control plants wilted in a few hours after being cut. ROSHARDT is inclined to think from these results that ether is absorbed and carried to the leaves, while the xylol is not carried to the leaves. He has performed other experiments on other species with these two substances with similar results.

In order to test further the truth of this hypothesis, ROSHARDT has performed experiments somewhat similar to those which I shall describe, the results of which appear in tables V, VI, VIII, and IX. He has interpreted his results, however, in an entirely different manner. Rooted plants of *Arum maculatum*, *Phaseolus multiflorus*, *Malva neglecta*, *Convallaria majalis*, and *Physalis alkekengi* were experimented upon; two similar plants of each species were placed in a PFEFFER'S transpiration apparatus. One plant was left undisturbed and a section of the stem was steamed for a certain time. The water absorbed was calculated in volumes, and the amount transpired was determined by weighing at regular half-hour intervals. The investigation was carried on until wilting began. In his table (p. 352) which represents his results on *Arum*, it will be noticed that the amount of water transpired during the first half-hour after treatment is 0.095 gm., while 0.110 gm. was given off during the second half-hour. During the 3rd, 4th, and 5th intervals, 0.090, 0.095, and 0.100 gm. respectively are lost. The succeeding periods also show some increases over the amount of water transpired during the preceding ones. It is noticeable that in the 6th interval no water whatever is given off. From these quantitative results ROSHARDT concludes that apparently neither poisons, nor displacement of the contents of the vessels, nor a stoppage of the tubes occur as a result of killing the stem with heat, but the final (though not continuous) decrease in the water transport is due to a lack of energy, which the dead cells are unable to supply.

EWART (14) adheres to the vitalistic theory, and, after repeating STRASBURGER'S experiment on a maple tree 15 m. high, concludes that picric acid is not a satisfactory poison for killing the stem

cells in such an experiment, owing to its retention in the walls of the wood vessels and its inability to diffuse well laterally. In an experiment in which the base of the trunk was first placed for 2 days in formic aldehyde, after which eosin was added to the solution, the latter rose to the top in 4 days. EWART finds, however, that in this case eosin rises not in the poisoned part of the wood, that is, the outer younger rings, but in parts which the formalin had not penetrated at all or only in very dilute form and which were still alive. Even in this case the flow of eosin solution was only temporary, nearly all conductivity being practically lost in 5 days. EWART concludes that his results apparently show that eosin solution following formalin instead of rising in the young poisoned portion of the wood passed upward through the unkilld parts. "The ascent of sap in trees must be regarded as a vital problem in which vital actions, directly or indirectly, take part," and is "a vital problem in so far as it depends upon conditions which hitherto can only be maintained in living wood."

REINDERS (23) found that manometers placed one above the other on the same stem behave quite independently of one another, sometimes one and sometimes another showing the lower pressure. In a suspended water column the pressure decreases gradually toward the top. On account of the differences of pressure observed in *Sorbus latifolia*, *Cornus*, and *Syringa*, REINDERS feels constrained to conclude that the living wood is normally able to pump water actively. The irregularities in his pressure measurements led him to seek for the cause in the activity of the living cells of the wood. He believes that the irregularities would disappear if these influences were removed; therefore he killed with steam a 2 m. stem of *Cornus* in two places for a distance of 10-12 cm., the distance between the killed portions being 66 cm. He also killed a 2.5 m. branch of *Sorbus* throughout its length, observing that the manometers at once showed more regularity; the leaves on this stem remained uninjured for 3 weeks. Four manometers were attached to the stem of a 2 m. *Syringa vulgaris* bush; the instruments after a short period all showed an equal "suction," which soon varied during the night and day, although the differences in pressure were small, a higher pressure sometimes being indicated in one and

sometimes in another. After 15 days a branch bearing one of the manometers was killed, together with a portion of the stem to which it was attached, by passing an induction current through them. After at first showing slight variations in pressure, this manometer followed the same periods as the others, but always "sucked" slightly more. REINDERS has given us only a preliminary account of his experiments, and the final report will be awaited with interest.

ZIJLSTRA (43), after having kept 50 cm. of the stems of a small apple tree and several plants of *Polygonum cuspidatum* and *Helianthus tuberosus* cooled to 0° C. 6-8 days, finds no fading of the leaves during that time, while leaves on cut branches hung in the neighborhood rapidly withered. In spite of this seemingly convincing result, he still believes that the living cells are necessary to sap-flow, as held by his associate REINDERS. His explanation is that it is quite probable that 50 cm. is too short a stretch to show conclusive results, although he did not take the trouble to treat longer portions. Both of these investigators, therefore, advocate the doctrine of a pumping action of the wood, as formulated by GODLEWSKI, for which the living cells are necessary. ZIJLSTRA allowed a solution of "säure violett" to ascend dead and living branches, and then examined them microscopically. In the living ones only the tori of the bordered pits were stained, together with a thin layer of the walls of the vessels. In the dead branches the whole of the wood was uniformly colored. He concludes, therefore, that the ascending water takes quite a different course in dead wood from that in living wood.

JOST (17, 18) points out that URSPRUNG's method of experimentation is an indirect one, and that, if it is not due to an increased evaporation in the scalded portion or to the stoppage of the vessels, which URSPRUNG was unable to find, then it must be due to the death of the parenchyma cells. He suggests that by heating the stem perhaps changes occur in the walls or in the contents of the vessels which one cannot readily observe with the microscope.

CZAPEK (7, 8) also doubts the worth of such experiments as described by URSPRUNG, since in the killed portion physical disturbances may be induced, such as drying out of the cells walls or

stoppage of the vessels, which in themselves would influence the passage of water even if the killed cells were otherwise capable of conduction. Both JOST and CZAPEK doubt whether all changes induced in the cells by heat can be seen with the microscope. The experiments of WEBER (40) on heated portions of *Picea excelsa*, in which he found that both boundaries of the treated region between the dead and living portions were unable to transmit water even under pressure, were confirmed and extended by JANSE (16). WEBER further detected a transparent substance in the vessels. The experiments tend to show that a stoppage of the vessels may occur in heated stems, and also that a partial poisoning of the leaves follows the death of the cells of the stem, since withering of the leaves begins before stoppage of the flow can be observed, as has been shown by DIXON.

In microscopically investigating the leaves of *Populus*, *Tilia*, *Syringa*, *Salix*, and *Acer* borne above a treated stretch, DIXON (10) found that the mesophyll and the walls of the tracheae of the leaves become discolored before wilting occurs, which led him to suspect that the leaves are dying from other causes than mere drying. ROSHARDT contends, however, that the discoloration of the mesophyll and veins is no more an indication of poisoning than it is of mere lack of water, and that the discoloration of leaves on a stem with a killed section is not nearly so general as DIXON implies. As further proof that injurious substances are caused by heating the stem, DIXON mentions instances of leaves wilting directly below the killed stretch. ROSHARDT states that in all of the 800 species which he treated he could not find wilting in any of the leaves below the killed portion. That substances can be forced downward by steaming the stem is shown by my observations on *Cyperus*. I have found that some vessels below the killed portions were often totally or partially filled with resinous substances, even as far as the roots. ROSHARDT, on the other hand, failed to observe such stoppages either above or below the heated region. As further evidence that substances may be forced downward, my observations on *Cyperus* show that when cut stems are placed in water and the stem heated, numerous air bubbles are forced out of the cut end by the treatment.

URSPRUNG (35-37) holds that DIXON's idea that poisonous substances are carried to the leaves from the heated portion cannot be the correct one, since he finds that poisons such as CuCl_2 cause fading in quite a different way from that which occurs in the case of leaves on heated stems, and very much more quickly than is caused by a decoction of the stem supplied to the leaves in the manner described by DIXON. I can see no reason whatever for supposing that a metallic poison should have the same effect as the toxins which may be engendered by heating the stem, nor that the time required should be the same in both cases. By placing the faded leaves of an *Impatiens* branch, which had stood in a decoction, in a moist atmosphere, URSPRUNG observed that they soon regained their turgescence. He thinks this shows that the leaves are not affected by plasmolyzing substances of a decoction of the plant. It may be, however, that these substances exert their plasmolyzing influences more slowly, and that the turgescence may be recovered if the leaves are not dead. It is well known that leaves may undergo a very marked degree of wilting and still recover their turgescence. SCHROEDER has shown that most leaves can lose as much as one-half of their water content without severely suffering.

SCHROEDER (27), in studying the symptoms of death as a result of wilting, finds that in most leaves a discoloration occurs, due to an oxidation of the tannin content. He also observed that in the early stages of death the chloroplasts move to one end of the cell or toward the middle; they round up and lose their typical color and structure. The protoplasts finally contract, the plastids take on a glassy appearance, and Brownian movements are observable in the cell contents. In the microscopical studies which I have made of the leaves on steamed stems, I have found many of the same conditions described by SCHROEDER, all of which indicates that these leaves are dying, not so much, it seems to me, from a lack of water as from the effect of some harmful substances. He finds that the rate of loss of water decreases from the beginning to the end of the process. The amount given off during any one interval is never greater than that of the preceding one. Death of the leaves greatly modifies the successively decreasing rate of water loss during wilting. The first 50 per cent of the fresh weight

of the leaf is usually very rapidly lost when dead, after which the amount decreases more uniformly.

JOST puts the question clearly in maintaining that "a completely convincing experiment must show that the leaves which are supplied with water by a dead stem are able to remain for a long time alive." The difficulty so far has been, in part at least, to render the living cells of a stem inactive without causing other changes, or only such as may be ignored. It has been observed by BOEHM (3) and STRASBURGER (30), among others, that in experiments in which certain portions of a stem are killed with steam, the leaves above these regions wither and die sooner than in the control, a phenomenon which KOSAROFF (20, 21) also observed in his experiments on cooled stems. That water passes through the scalded or cooled region has been shown many times by placing cut ends of the stems in dyes. That it does not pass in sufficient quantities may perhaps be the cause of the earlier withering of the leaves on a branch, a section of which has been killed, as has been urged by URSPRUNG, EWART, and by ROSHARDT in support of the vitalistic theory of sap-flow. URSPRUNG employed steam and low temperature to kill sections of the stem in certain woody plants, or removed the bark without otherwise disturbing the connection between root and stem. In addition to steam, ROSHARDT has used low temperature, and in certain cases xylol or ether. According to these authors, earlier withering of the leaves is a sure sign that a sufficient water supply does not pass through the killed portion. Both authors have shown that the longer the killed portion is, the more quickly the leaves above wither and fade, as was formerly observed by JANSE (16).

That SCHWENDENER (29) still adheres to the vitalistic hypothesis of sap-flow is shown by certain passages in the last edition of his lectures on mechanical problems in botany, in which he says:

Ohne dieses Eingreifen (Lebensthätigkeit der Zellen) ist die Hebung des Wassers auf Höhen von 150–200 Fuss und darüber einfach unmöglich und alle Bemühungen, die vorhandenen Schranken mit unklaren physischen Annahmen zu durchbrechen, sind nicht viel mehr als ein Suchen nach dem Stein der Weisen.

LECLERC DU SABLON (22) believes that the ascent of sap is easily explained by the osmotic qualities of the living cells of the

leaves, stems, and roots. The transpiration of the leaves and the absorption by the roots sets up a difference in pressure at the two ends of the plant. The principal factor, however, in the ascent of sap is the osmotic power of the wood parenchyma, which tends to keep the quantity of water constant. He thinks that transpiration simply serves to accelerate the rate of flow, but does not cause it ("Le mécanisme des mouvements de la sève est donc le même dans un arbre haut de 100 mètres que dans une herbe de quelque centimètres, dans une tige verticale que dans une tige horizontale").

DIXON's theory of sap-flow is perhaps the most thoroughly in accord with the experimental facts as they stand today. He holds that the elevation of water even in the highest trees is due to a tensile stress being set up in the tracheae of the leaves when water is abstracted from them by the evaporation from the leaves, which stress is transmitted to the water in the larger vessels. The water adheres to the walls of the vessels, so that the stress is resisted. The water "hangs" in the vessels "by virtue of its cohesion." This theory has been objected to on the ground that the water columns are not continuous, and that air bubbles and vapor are present in the vessels. DIXON points out that owing to the permeability of the walls of the vessels, the water does form a continuous system. It will be seen that this theory eliminates the action of the living cells of the stem. DIXON cites the classic experiments of STRASBURGER (31) in which an oak 22 m. high was sawed through and placed in picric acid for three days until the liquid had risen 3 m. The tree was then placed in fuchsin, which rose 18 m. in the dead stem in 8 days. DIXON believes that this experiment proves conclusively the uselessness of the living cells of the stem in sap-flow.

Preliminary experiments

It is plain that the question as to the effect of killing a section of a stem on the character and quantity of the sap-flow is still unsettled as to many particulars. There is no question that, as URSPRUNG admits, such stems conduct a certain amount of water for a considerable period of time. Experiments conducted on a quantitative basis are essential in such a problem, and the following studies have been carried on from this standpoint. After

several years of experience with classroom experiments, it has been found that the common umbrella plant, *Cyperus alternifolius*, is a very suitable species for such experimentation. The plants are easily cultivated in the greenhouse, often reaching 60–90 cm. or more in height. The aerial stems are free from nodes and leaves except at the top, where the large, many-rayed involucre of narrow leaves is situated. The younger leaves are comparatively translucent, permitting easy observation of the rise of colored liquids such as eosin solutions. As will be seen below, the plants transpire rather rapidly as compared with those in ordinary use for laboratory experiments, giving off fairly large quantities of water per unit area of leaf surface. The rate of sap-flow is of course correspondingly rapid. Further, the stems and leaves are not easily injured by the mechanical manipulation often necessary in such experiments. *Cyperus papyrus* is also an excellent plant for comparative study on account of its longer stems, but the fading of the leaves is less readily observed, owing to their narrow threadlike form.

The character of the involucre leaves allows a glass tube or LIEBIG condenser of suitable diameter and length to be readily slipped over the crown and down on the stem without injury to any part of the plant. Two-holed rubber corks may be split and clamped about the stem above and below and fitted into the glass tube. If small glass tubes are bent at right angles and inserted into the remaining holes of the corks, an inlet and outlet for steam is easily arranged. The steam may be conducted away to any distance so as not to injure the plants except in the desired region. The method of arranging the experiment is shown in fig. 1. By clamping the rubber connections and leaving the incasing glass tube on the plant after treatment, the stem is inclosed in a sterile chamber and is kept in a moist atmosphere which prevents its drying and does away with the necessity of using paraffin or other protective covering. If it be desired to use melted paraffin or wax, this may be poured into the tube, thus inclosing the injured region. In using a poison instead of steam, the fluid may be poured into the tube at the top and drawn off at the bottom after the treatment is finished. I have successfully used grafting wax to further secure the corks and connections and prevent

poisonous solutions from leaking out and injuring the stems below the chamber. Such an arrangement has the added advantage of allowing the treated portion of the stem to be easily observed



FIG. 1.—Photograph of *Cyperus* plant having all but one leaf removed and growing in a nutrient solution; this photograph shows the incasing glass tube and connections arranged for steaming a portion of the stem.

the zone between the killed and living region, in order to determine if possible whether any visible plugging or stoppage of the vessels or other changes above the killed zone occur. Microscopic examinations were also made to determine to what extent poisons penetrated the cells of the stems and the leaves as indicated by

during the experiment. For killing sections of the stem I have used steam, hot wax, and several poisons, treating sections of the stems for any desired length. As poisons I have employed saturated aqueous solutions of picric acid, mercuric bichlorid, copper sulfate, potassium hydroxid, 1 per cent aqueous solution of chromic acid, 4-40 per cent formalin, alcohol, xylol, chloroform, and ZENKER'S fixing fluid. In every instance I have killed both shorter and longer stretches of the stems, and have compared the time required for the withering of the leaves, and the amount of water absorbed and given off, with the same data from an untreated control plant cut and standing with its base in water. I have also made some microscopic examinations of the stems above and below the killed portions, especially in

their plasmolysis. I have further experimented in the same way with cut stems, in order to compare the amount and rate of transpiration with that of stems treated in the same way but kept in connection with the roots. Since several recent workers have raised objections to the use of cut plants in such experiments, this point is worthy of careful consideration. Throughout the investigation, all plants were kept as nearly as possible under similar conditions of light, temperature, and moisture.

To determine the amount of water lost per unit area of leaf surface by the umbrella plant as compared with other common forms such as *Helianthus annuus*, potted plants and plants grown in culture solutions were used. In such experiments all of the stems but one were cut away, and the soil and pot were then so inclosed as to allow no loss of water except through the leaves. In case of plants grown in culture solutions the corks were sealed in. For these cultures 500 c.c. wide-mouth bottles were used. Flat corks to fit were split and fitted about the stems of the plants after they had first been wrapped with cotton wool for protection. The corks were sunk about 1 cm. below the edge of the bottle, so that melted wax could be poured in when it was desired to seal in the corks. The plants were grown in KNOP'S nutrient solution as given by DETMER. Leaf areas were determined by using EASTMAN'S ferro-prussiate paper; the white areas were cut out and weighed. By obtaining the weight of 1 sq. cm. of the blue print paper, the areas of the leaves were easily obtained. In order to determine whether the paper was uniform in weight, several weighings were made. The average weight of 1 sq. cm. was used as the unit in calculating the leaf areas. This of course must be doubled in determining the transpiring area if stomata are on both sides of the leaves, which is not the case in the normal plant. In order to calculate the rate of motion of the transpiration stream, the lithium method as described by SACHS (25) for rooted plants, as well as the eosin method, was used. In the latter case the rise of the eosin in the stems and leaves of cut branches was observed, as is easily possible in the umbrella plant by the aid of the horizontal microscope.

Some of the experiments described by URSPRUNG and ROSHARDT

have been repeated, with similar results. Some experiments have also been made on plants other than *Cyperus*, but in this paper my description will be confined to this plant.

SAMPSON and ALLEN (26), in studying the influence of external factors on transpiration, have found that “variation in the transpiration per unit area for a given time is found to be slight for plants of the same species, when about the same age, and grown and tested under similar conditions”; facts which my observations on *Cyperus* fully substantiate.

The following table (I) shows the variation in the total daily amount of water lost in *Cyperus* plants of nearly the same age and size when grown and tested under our greenhouse conditions. The 5 plants in each series were selected with reference to likeness, and the weighings were made at the same time for 10 days, the average of which was taken as the average daily transpiration loss. The average daily temperature was calculated from the daily record of a self-registering RICHARD thermograph placed in the neighborhood of the plants. This is necessary, since the changes in temperature affect the transpiration rate to a very marked degree. The plants in series I were young, with their involucreal leaves just expanded; those in series II were well developed, dark-green plants.

TABLE I
SHOWING VARIATION IN AMOUNT OF WATER LOSS BY PLANTS OF APPROXIMATELY THE SAME AGE AND SIZE

SERIES I			SERIES II		
No. of exp.	Average daily water loss in grams	Average daily temperature	No. of exp.	Average daily water loss in grams	Average daily temperature
1.....	4.5	24° C.	1	1.8	20° C.
2.....	4.7	24° C.	2	1.9	20° C.
3.....	5.0	24° C.	3	1.6	20° C.
4.....	4.6	24° C.	4	2.0	20° C.
5.....	4.2	24° C.	5	1.7	20° C.

I have determined by the pot method and by means of plants grown in nutrient solutions that the average amount of water transpired per unit area for a given time is 4–10 mg. per sq. cm. per hour during a period of 24 hours. In comparison with the earlier

observations of SACHS on the amount of transpiration in *Helianthus* (about 2.23 mg. per sq. cm. per hour) and with those of more recent investigations, it is evident that *Cyperus* may at least be regarded as a rapidly transpiring plant under greenhouse conditions. Miss CLAPP (6), in comparing a number of common plants as to transpiration, found that *Helianthus annuus* stands far ahead of the 30 other forms which she investigated. A plant with a total leaf area of 5.056 sq. cm. gave off on the average 25.7 mg. of water for each sq. cm. of leaf surface per hour under ordinary greenhouse conditions. Hence *Cyperus* gives off a much smaller amount of water per unit area of leaf surface per hour than does *Helianthus*.

The leaf stems have numerous stomata over their surfaces, while these structures are confined almost entirely to the under surfaces of the leaves. By removing the involucres of plants grown in nutrient solutions and sealing the cut ends of the stems with grafting wax, then making weighings, the daily transpiration per unit area of stem surface was found to be on the average about 3.5 mg. per sq. cm. per hour. After having measured the average daily water loss of a plant in culture solution through its leaves and stems, the involucre was removed, the cut ends sealed, and weighings resumed for several successive days.

TABLE II
SHOWING AMOUNT OF DAILY WATER LOSS BY A PLANT BEFORE AND AFTER
REMOVING THE LEAVES

PLANT WITH LEAVES			PLANT WITH LEAVES REMOVED		
Days	Daily loss in grams	Average temperature	Days	Daily loss in grams	Average temperature
1.....	17.4	23° C.	1	2.2	25° C.
2.....	19.9	25° C.	2	2.1	23° C.
3.....	18.1	24° C.	3	2.1	24° C.
4.....	18.6	24° C.	4	2.2	25° C.
5.....	19.4	25° C.	5	2.2	25° C.
Average daily transp. loss 18.68 grams			Average daily transp. loss 2.18 grams		

The data tabulated in table II were obtained by using a large, well rooted plant growing in a nutrient solution. The stem was 35 cm. long, 4 cm. in diameter, bearing an involucre of 17 large rays.

The temperature was obtained by averaging the daily record as registered by a RICHARD thermograph. It is seen from the table that a plant giving off 18.6 gm. of water per day through its leaves and stem will transpire 2.2 gm. only through its stem.

Observations with lithium nitrate show that water rises in stems of plants in nutrient solutions whose tops have been removed, at the rate of about 150 mm. per hour. SACHS (25) concluded that the transpiration current travels at the rate of 63 cm. per hour in *Helianthus annuus*, and that the rate of sap-flow varies greatly in different plants and in the same plant under different conditions. The method of measuring the rate of sap-flow by setting cut stems in dyes and observing the rise of the colored solution has been criticized by SACHS, who showed that the water travels faster than the dye. A more exact method used by him consists in watering the entire plant with a solution of some lithium salt, or adding the salt to nutrient solutions, and ascertaining by means of the spectro-scope how far the salt rises in a given time, thus obtaining the rate of flow.

TABLE III

SHOWING THE RATE OF SAP-FLOW IN ROOTED PLANTS AS DETERMINED BY SACHS'S LITHIUM METHOD

Length of plant	Time taken to ascend	Rate per minute	Rate per hour
73 cm.	24 min.	3.04 cm.	182.4 cm.
50 cm.	20 min.	2.50 cm.	180.0 cm.
45 cm.	15 min.	3.00 cm.	180.0 cm.
48 cm.	17 min.	2.82 cm.	145.2 cm.
52 cm.	20 min.	2.60 cm.	156.0 cm.
41 cm.	15 min.	2.73 cm.	163.8 cm.
36 cm.	13 min.	2.76 cm.	165.6 cm.
29 cm.	10 min.	2.90 cm.	174.0 cm.
60 cm.	15 min.	4.00 cm.	240.0 cm.
47 cm.	12 min.	3.91 cm.	234.6 cm.
35 cm.	10 min.	3.50 cm.	210.0 cm.

In obtaining the data tabulated in table III, I have employed SACHS's lithium method, and find that the rate of sap-flow in potted *Cyperus* plants and of plants in nutrient solutions varies from a minimum of 145 cm. per hour to a maximum of 240 cm. per hour. In cut plants the flow is slightly more rapid, the extremes being 180 and 250 cm. per hour. In comparison with *Helianthus*,

therefore, the rate of sap-flow in *Cyperus* is exceedingly rapid. Certain other herbaceous plants, however, have been reported as having a still more rapid flow, STRASBURGER observing that the rate of rise was 6 m. per hour in *Bryonia* and *Cucurbita*. We see, therefore, that *Cyperus* may at least be regarded as a rapidly transpiring plant, that its transpiration stream is correspondingly rapid, and that the amount of water given off from plants of relatively the same age and development show very little variation.

Experiments with heat

Over 200 experiments in which portions of the stems were killed with steam have been performed and the results carefully compared. The results of all of them are substantially in accord. The results obtained in several representative experiments are tabulated in table IV.

In table IV the numbers in the first column on the left refer to the actual numbers of the experiments performed; for example, 6—S (1908) means the sixth experiment in 1908 in which a portion of the stem (20 cm. in this case) was killed with steam. Each year the experiments performed were numbered anew. In the second column the length of the stem from the soil to the involucre is tabulated. The length of the steamed portion varies from a minimum of 5 cm. to a maximum of 30 cm., as will be seen from the third column; the time of treatment was 10–30 minutes. In the fourth column the actual day and month when the steam was applied are shown. The plants were in all cases grown in pots in soil under favorable greenhouse conditions. The control plants were stems cut from the same pot as the one which had been treated, and were approximately of the same size and age. They were set in water in the neighborhood, and the time of wilting of the leaves compared with those of a killed plant. As is well known, the leaves on cut stems of this plant not placed in water wither within 24–48 hours. I have omitted from this table the distance above the base of the stem at which the steam was applied, since I have found that it makes no appreciable difference whether it is applied near the leaves or lower down.

It is plain that the leaves of umbrella plants which have a portion

TABLE IV

SHOWING RESULTS OF KILLING 5 TO 30 CM. OF THE STEM WITH STEAM, AS
COMPARED WITH UNTREATED PLANTS CUT AND SET IN WATER

No. of exp.	Height of stem	Length of steamed portion	Time of treatment	Date	Results and comparisons
6—S (1908)	30 cm.	20 cm.	15 min.	Jan. 20	Leaves remained perfectly fresh and turgid for 7 days; Jan. 28 began to droop; withered Jan. 30, or in 10 days from time of treatment; control plant, cut and set in water, withered in 8 days.
11—S (1908)	40 cm.	15 cm.	15 min.	Feb. 2	Fresh and turgid for 8 days; Feb. 11. showed signs of withering; entirely wilted Feb. 13, or after 11 days; control plant in water withered in 6 days.
14—S (1908)	20 cm.	10 cm.	15 min.	Mar. 5	Fresh and turgid after 8 days; March 13, began to wither; entirely withered March 18, after 13 days; control in water withered in 8 days.
50—S (1908)	15 cm.	10 cm.	15 min.	June 15	Perfectly turgid after 8 days; withered June 24; dry June 26; control plant in water dry in 8 days.
5—S (1909)	20 cm.	10 cm.	15 min.	Mar. 15	Results exactly the same as in exp. no. 14—S (1908), except control in water was entirely dry in 7 days.
24—S (1909)	35 cm.	10 cm.	20 min.	April 5	Turgid for 8 days; withering April 15; entirely withered April 16, or after 10-11 days; control in water dry in 9 days.
31—S (1909)	25 cm.	15 cm.	20 min.	April 11	Withered on 11th day, April 22; control in water turgid for 9 days.
48—S (1909)	45 cm.	15 cm.	20 min.	April 19	Fresh and turgid for 10 days; withered April 30; control in water turgid for 9 days.
56—S (1909)	40 cm.	20 cm.	30 min.	April 22	Remained fresh for 4 days; April 27, showed signs of withering; next 2 days rapid withering; April 30, quite dry; stem turgid above and below steamed part, but collapsed in tube where steamed; no controls.
62—S (1909)	52 cm.	30 cm.	15 min.	May 3	Showed decided withering in 3 days; entirely withered in 5 days and dry in 7 days; control in water turgid for 7 days and dry in 9 days.

TABLE IV—*Continued*

No. of exp.	Height of stem	Length of steamed portion	Time of treatment	Date	Results and comparisons
20—S (1910)	43 cm.	14 cm.	15 min.	Feb. 13	Remained turgid for 7 days, then leaves drooped, edges inrolled, and plant dried in 10 days; control in water withered in 6 days.
27—S (1910)	51 cm.	17 cm.	15 min.	Feb. 19	Remained turgid for 8 days; several leaves drooped on 9th day; dry in 7 days; control in water turgid for 7 days.
41—S (1910)	32 cm.	20 cm.	15 min.	Mar. 4	Turgid for 7 days; leaves drooping on 8th day, dry on 9th day; control in water withered in 7 days.
52—S (1910)	41 cm.	11 cm.	15 min.	Mar. 22	Turgid for 8 days, drying on 10th day, withered on 11th day, dry on 13th day; control in water withered in 8 days.
63—S (1910)	60 cm.	10 cm.	15 min.	Mar. 22	Fresh and turgid for 8 days, drooped on 9th day, and dry in 11 days; control in water withered in 8 days.
74—S (1910)	32 cm.	20 cm.	20 min.	April 16	Withered in 7 days, entirely dry in 8 days; control in water withered in 7 days.
101—S (1910)	58 cm.	25 cm.	22 min.	May 2	Wilted in 4 days, dry in 6 days; control in water withered in 7 days.
109—S (1910)	61 cm.	20 cm.	25 min.	May 11	Leaves drooping in 7 days, withered in 8 days, dry in 9 days; control in water; withered in 6 days, dry in 7 days.
121—S (1910)	32 cm.	8 cm.	15 min.	May 23	Drooped in 10 days, withering in 11 days, dry in 12 days; control in water withered in 6 days.
133—S (1910)	42 cm.	5 cm.	20 min.	June 7	Leaves turgid and fresh after 10 days except tips very slightly drying, withering in 16 days, dry in 18 days; control in water withered in 8 days.
137—S (1910)	52 cm.	28 cm.	10 min.	June 15	Withering on 5th day and drying on 6th day; control in water withered in 7 days.

of their stems killed with steam remain turgescient for a considerable time, and do not wither quite so quickly as those on stems cut and set in water. On treated stems the leaves remain turgescient 5-18 days, while on stems cut and set in water they remain turgid

for a period not to exceed 9 days. The longer the steamed portion of the stem is, the sooner the leaves above lose their turgidity, wither, and dry. This is conspicuous in the cases of the plants in experiments 6—S (1908), 56—S (1909), 62—S (1909), 27—S (1910), 74—S (1910), 101—S (1910), 109—S (1910), and 137—S (1910), as compared with the others in which shorter sections were killed, as in 14—S (1908), 50—S (1908), 5—S (1909), 24—S (1909), 63—S (1910), and especially 133—S (1910) and 137—S (1910).

When plants of *Cyperus* have a portion of the stems steamed, the leaves above show no immediate effect. After some time, depending upon the length of the stretch heated, the involucre rays usually begin to droop, closing more or less about the stem. Loss of turgidity then follows, the margins of the rays become rolled inward, and dryness supervenes. In some cases discoloration follows the treatment, the leaves becoming spotted. This discoloration usually takes place at the tips first, but may occur also at the bases of the rays. I have noticed that this discoloration is dependent upon the length of the stem killed. When very short portions are steamed, the leaves usually wither and dry without discoloring, behaving like those on cut stems in this respect. When, on the other hand, longer portions are heated, discoloration usually follows. This fact seems to me to indicate, as DIXON maintains, that poisonous substances may be carried to the leaves from the killed portion.

In comparing the above results with those of experiments on Gramineae as described by ROSHARDT, in which 10 to 20 cm. of the halms were steamed, *Cyperus* appears to be able to retain the turgidity of its leaves after such treatment about as long as any of the grasses. The leaves finally droop at the bases, so that the whole involucre closes about the stem like the ribs of a closed umbrella. This is always the first sign that the plant has suffered from the treatment; yellowing of the tips and bases may also occur; and finally the leaves dry out after, in some cases, assuming a drooping position. In some instances the edges of the drying leaf become inrolled. Perhaps the initial drooping of the leaves or loss of turgidity may be due to some toxic action initiated by the treatment. Leaves on cut stems of *Cyperus* lose their turgidity and

droop in 1-2 hours, and very soon become dry, agreeing in this respect with the behavior of the leaves of *Bromus hordeaceus*. My observations support ROSHARDT's conclusions on this point.

By the method described above, plants growing in nutrient solutions may be conveniently sealed in the culture bottles without harming the plants, and the amount of transpiration from day to day may easily be determined by weighing. In order to ascertain whether less water is carried to the leaves after steaming, the rate of transpiration during each 24 hours for 5 days was determined, changes of temperature and the weather conditions being noted; then 10 cm. of the stem were killed with steam and the observations on rate of transpiration were continued. I have tabulated (tables V and VI) the results of such a series of observations.

TABLES V AND VI

SHOWING THE EFFECT ON AMOUNT OF WATER LOST DAILY BEFORE AND AFTER STEAMING 10 CM. OF STEM

TABLE V—OBSERVATIONS BEFORE STEAMING				TABLE VI—OBSERVATIONS AFTER STEAMING				
Date 1910	Loss in grams	Average tem- perature	Weather conditions	Date 1910	Loss in grams	Average tem- perature	Weather conditions	Remarks
May 18	4.0	24° C.	Clear	May 23	1.7	18° C.	Cloudy	Plant in good condition.
May 19	4.7	24° C.	Clear	May 24	1.5	25° C.	Cloudy	Stem above killed part withering.
May 20	5.8	25° C.	Clear	May 25	0.9	19° C.	Cloudy	Leaf tips very slightly drying.
May 21	3.2	39° C.	Cloudy, warm	May 26	0.7	20° C.	Clear	Leaves withered, dry, and in-rolled.
May 22	2.9	18° C.	Very cloudy	May 27	0.4	23° C.	Clear	Leaves entirely withered and dry.
Average transpiration in 24 hours=3.9 grams.				Average transpiration in 24 hours=1.04 grams.				

In tables V and VI the date of the observations is indicated in the first column, May 18-22, 1910 (before steaming 10 cm.), and May 23-27, 1910 (after steaming). In the second column the loss in grams before and after treatment is shown. There is a gradual decrease in the transpiration loss from 4 gm. to 2.9 gm. per day in table V, due probably to gradual lowering of the temper-

ature. The temperature was obtained, as previously, by taking the average of the temperatures recorded by the self-registering thermometer. After steaming, the diminishing transpiration cannot be due to decrease in temperature, since the temperature on the first day after killing the stem was the same as on the last day before steaming 10 cm. In table VI the average daily temperature gradually rises, while the transpiration diminishes from day to day, until on the last day (May 27) it is only 0.4 gm., having fallen off from 1.7 gm. on May 23. The weather conditions are recorded in order to show that decrease in transpiration is more dependent on the stem having been steamed than upon the changes of temperature and light.

It is evident from these tables that the amount of water transpired after steaming 10 cm. of the stem of *Cyperus* is very much less than before the treatment. The difference in temperature and weather conditions must be taken into account, but they are probably not sufficient to account for the very great difference in the amount of water given off in the two cases. In table V the average temperature record is higher than in table VI, and there was more clear weather, but these differences do not account for the immediate and continued slowing down of the transpiration rate as shown in table VI. The amount (1.7 gm.) transpired during the first 24 hours after steaming is far below that of any corresponding period before treatment. On a very cloudy day, at a temperature of 18° C., the plant gave off 2.9 gm. of water; while on a very bright day, at a temperature of 25° C., it transpired only 1.5 gm. after a section of 10 cm. had been steamed. It is plain that steaming 10 cm. of a stem of this plant very soon affects in some way the amount of water given off by the leaves.

In fairly mature shoots of *Cyperus*, the amount of water given off by the leaves in a given time may be assumed to be approximately equal to the amount absorbed by the roots. Therefore, the steaming must in some way interfere with the amount of water that passes through the killed portion, as well as that given off by the leaves. There is of course an almost immediate withering and shrinking of the steamed portions of the stem; if this region is exposed it soon dries out also. Careful weighing shows that

fresh turgid leaves of this plant contain about 80 per cent of their dry weight of water, while drying leaves on steamed stems directly after treatment, that is, 2-3 days, contain only about 50 per cent. As further noted in the table, the drying and withering proceed gradually, the leaves first drooping at their bases. There can be no doubt that steaming a section of stem reduces the water supply to the leaves, and that they thus come to contain less water. Whether this is the cause of withering, however, is not altogether clear. It may well be that there is water enough to maintain turgidity, even though the total amount has been reduced.

DIXON (9-12) concludes from experimental and histological evidence that the initial stages of fading are caused by a poisoning of the mesophyll cells of the leaves, while the final stages are accelerated by a clogging of the walls and a stoppage of the lumina of the conducting tubes. Upon microscopical examination of the steamed region, no visible disorganization of the cells except in the peripheral parenchyma could be found. In these cells the protoplasts were collapsed and the chloroplasts were discolored. The vascular bundles and internal parenchyma appear normal. When such stems are cut off and set in eosin, however, the color does not appear alone in the bundles, but diffuses out into the surrounding tissue. Since in these experiments the stem has been confined in a sterile chamber, there is no chance for the action of bacteria, and I have failed to find bacteria present in the tissues after a period of 10 days. Although no visible disorganization in this region can be made out with the microscope, it does not follow that disorganization has not occurred, and that certain decomposition products may not be exuded into the transpiration stream and be carried to other parts of the plant.

When steamed stems are split lengthwise, even without the aid of the microscope numerous dark streaks or lines in the tissues may be seen reaching as much as 15-20 cm. above the killed portion and often as far as the leaves. When the leaves are held up to the light, dark streaks can also be seen along some of the veins. I have studied both cross and longitudinal sections of the stems both above and below the steamed region. Under the microscope these streaks are seen to be vascular bundles, which

have been colored yellow or brown; the whole bundle is colored a yellowish brown or black. Nearly every bundle for some distance above the killed portion presents this appearance, while only occasionally one or more are seen colored below the region. The phloem is the part most deeply colored, being very dark brown and often almost black. A disorganization of the substances in the sieve tubes has apparently been caused by the heat; these substances can be seen to have penetrated the cell walls and to have passed out into the other elements of the bundle and also into the parenchyma cells. Under the microscope the substance which plugs the vessels appears like the mucilage or gum-resin so often present in liverwort gametophytes. It is yellowish in color and gelatinous in consistency; on testing with alkanin it is found to give the characteristic red reaction of resin. The xylem vessels also appear to be plugged with this same resinous substance. The smaller pitted vessels as well as the larger ones show this plugging, also the spiral and annular vessels, and even the large air spaces. It varies in degree; sometimes all of the xylem will be stopped, and then again only one or more vessels. The walls of the vessels also show the presence of this substance, and it is even present for some distance out in the surrounding parenchyma cells. When unstained with alkanin it is yellow or brown, depending upon the amount present; the deepest color is in the phloem, where it is nearly black, which goes to show that the substance originates here and diffuses out into the surrounding tissues. That it is not present in the killed portion itself is probably due to the fact that the heat vaporizes or expands the liquids and forces them upward and downward in the sieve tubes, and that the lateral diffusion into the surrounding tissues occurs later. This substance becomes visible very soon after steaming the stem.

From the above observations there can be no doubt that in this plant substances due to steaming are exuded into the water passages, which may possibly obstruct the upward flow of water and prevent an adequate amount reaching the transpiring leaves above. These facts alone may possibly be sufficient to account for the diminished transpiration and diminished water content of the leaves indicated in tables V and VI. Whether this clogging accounts wholly for

the withering and final drying of the leaves, as has already been suggested by DIXON, is a difficult question. Although URSPRUNG and ROSHARDT were unable to observe such clogging substances in all of the plants experimented upon by them, they are entirely too conspicuous to be disregarded in *Cyperus*. DIXON (10) has also found clogging substances in *Populus* stems which have been treated with steam or hot water.

I have also made experiments using decoctions of the stems of these plants as a water supply. After thorough sterilization of the decoction, cut stems were set in it. In a very short time the xylem becomes plugged for some distance with the same resinous substance, judging from its reactions to alkanin, as stops the passages when steam is applied to a normal plant, while the phloem remains unstained. The leaves above soon lose their turgescence and rapidly fall off in the amount of water transpired.

When fresh stems are set in water, the xylem vessels finally become plugged with dark-colored material, which is probably a decomposition product, due to decay or bacterial action. In order to be sure that the plugging of the stems set in the decoction was not due to bacteria, as URSPRUNG believes to be the case in DIXON's experiments, I have examined both the solutions and the stems for the presence of bacteria and always with negative results.

To further test DIXON's hypothesis that heating a section of the stems causes substances to be formed which poison the plant, I have performed a series of experiments as follows. Nutrient solutions were made, in which a sterilized plant decoction instead of distilled water was used and the requisite salts added thereto. Plants grown in such nutrient solutions very soon show signs of fading and the leaves become discolored, behaving in all respects much like those with steamed stems. A plant was sealed in such a culture solution on June 3 and kept under the most favorable conditions; the bottle was sealed to keep the solution sterile. In 3 days thereafter the leaves began to droop, and in 5 days began to show signs of discoloration along the veins; in 7 days the leaves were streaked with yellow and appeared like those on steamed stems. A control plant, which was set up in an ordinary nutrient solution in the same way at the same time, remained perfectly normal. The con-

ditions were identical with the exception of the use of the decoction in making up the nutrient solution.

Sections were made of the leaves from a stem killed as just described. The protoplasts of the mesophyll cells were much contracted and the chloroplasts were discolored. The same thing is true of the leaves on a stem which has stood for some time in a sterilized stem decoction. The leaves from plants grown in a stem decoction also show similar appearances. All of my observations go to show that the plant after steaming is poisoned. DIXON (10) finds that discoloration of the leaves above the killed portion, and even on a separate branch if its water supply must pass through such a heated region, may occur. This he thinks is due to a poison, since leaves which wither simply from lack of water shrivel while they are still green. In *Cyperus* I have observed no such marked discoloration of leaves before shriveling. In many cases the leaves on a steamed stem dry without any discoloration whatever, although the protoplasts of the mesophyll may be completely plasmolyzed long before shriveling occurs. In other cases the leaves become discolored.

URSPRUNG believes that experiments with cut branches are untrustworthy in such problems as the one under consideration, since the conditions are not the same as when the plant is in connection with the roots. I have made a series of experiments to compare the results with cut branches with those obtained from rooted plants. The average daily rate of water loss was obtained for each stem, and then a portion of the stem killed with steam or hot wax and the weighings continued. That these cut stems behave like those in connection with the roots the following results will show. A section 10 cm. long of one of two similar cut stems, each of which gave off approximately 7 gm. of water in 24 hours, was steamed for 30 minutes; during the next 24 hours this amount decreased to 3.2 gm., and to 0.5 gm. in the third period, and the leaves were very dry. A control plant transpired 5.2 gm. during the first 24 hours, 4.7 gm. during the second 24 hours, and 4.2 gm. during the third period. We see that in cut plants there is the same immediate and continued falling off in transpiration after steaming the stem as occurs when the stem is similarly treated

but left connected with the roots. A section of the stem 10 cm. long of one of two similar cut plants whose daily water loss was 5.4 gm. was immersed for 20 minutes in hot wax, which was allowed to cool about the stem. This plant gave off 5.6 gm. of water during the next period of 24 hours, an actual increase over the amount given off before treatment; the control gave off 5 gm. during the same period. During the third period the plant with the dead section of stem gave off 1.8 gm. of water, and the control 2 gm. It seems evident from these results that steam has the same effect on the transpiration of cut stems set in water that it does on normal plants.

Judging from the behavior of the leaves on a stem with a steamed section, from the collapse of the mesophyll cells, and from the apparent disorganization induced by steaming as indicated by the plugging of the water passages, I have been led to conclude that this method of killing the cells is not a satisfactory one in order to settle the question as to the relation of living cells to sap-flow. I agree with CZAPEK that the killing of the cells should be accomplished without further disorganization of the transpiring tissues. I have tried, therefore, to find a more satisfactory method of killing the cells of the stem without causing so much disturbance and disorganization as is induced by steam. I have surrounded the stem in the region to be killed with hot paraffin or wax, by pouring it into the incasing glass tube at a temperature of 110° C. and allowing it to cool and set about the stem, thus killing it and protecting it during the experiment. In some cases I have found it necessary to protect the stem further with grafting wax. On microscopical examination I find that the portions thus treated are quite dead, the parenchyma cells having their protoplasts contracted, and the peripheral mesophyll cells being discolored, with their protoplasts contracted. No change could be observed in vascular bundles. In such stems when cut and set in eosin, the color passes up mainly in the tracheae, and does not diffuse laterally into the surrounding tissue as in steamed stems. I also find that much less plugging of the vessels above the killed portion occurs after this method, as well as less plasmolysis of the mesophyll cells. In every respect I think this method of applying heat is far superior to steaming,

though some plugging of the lumina occurs. I have tabulated (table VII) the results obtained by this method for comparison with those obtained in experiments with steam.

TABLE VII

SHOWING RESULTS OF KILLING CERTAIN PORTIONS OF THE STEMS WITH WAX HEATED TO 110° C. AS COMPARED WITH UNHEATED STEMS CUT AND SET IN WATER

No. of exp.	Height of stem	Length of killed portion	Date	Results and remarks
1—W (1910)	65 cm.	6 cm.	May 7	Leaves began to wither May 23, after 16 days; control in water dry in 5 days; wax relaxed about stem, exposing it to drying.
2—W (1910)	60 cm.	12 cm.	May 7	May 23, leaves slightly drooped but perfectly turgid; May 25, leaves quite drooping, tips drying and inrolling; May 26, leaves drying and inrolled; dry after 19 days, cut off for examination; control same as in no. 1—W.
3—W (1910)	50 cm.	10 cm.	May 19	June 11, leaves drooping; tips slightly inrolled; withering June 16; involucre dry after 23 days; control in water dried after 7 days.
4—W (1910)	53 cm.	10 cm.	May 19	Leaf tips drying and inrolling, slightly yellow; wax relaxed about stem; dry after 14 days; cut off for examination; portion above killed region showed yellow streaks about bundles, but no plugging of the lumina; control same as in no. 3—W.
5—W (1910)	50 cm.	40 cm.	May 19	May 20, some leaf tips drooping; May 23, leaves beginning to dry; May 25, plant dry, after 5 days only; cut off stem and set in eosin, color rose in vessels only; no visible plugging of lumina; control same as in no. 3—W.
6—W (1910)	30 cm.	20 cm.	May 22	June 2, leaves beginning to dry; June 3, leaves quite dry; June 5, leaves entirely dry; control in water dry in 7 days.
7—W (1910)	40 cm.	10 cm.	May 22	June 6, involucre still turgid, but 3 rays beginning to turn yellow, other leaves perfect in color; June 18, all leaves yellowing; June 20, plant quite dry; control dry in 8 days.
8—W (1910)	34 cm.	5 cm.	May 22	June 9, plant still in perfect condition except the portion killed; all of the leaves green and turgid and none show the slightest signs of injury or discoloration; at this writing (48 days after treatment) leaves show no signs of wilting; control dry in 8 days.

Experiments in which steam was employed to kill certain stretches of the stem, as indicated in table IV, show that the leaves

above such steamed regions remain turgescient for a period of 5-18 days, depending on the length of the stretch killed. Comparing the results of table VII with those of table IV, we see that in killing by hot wax, the longer the killed section, the sooner the leaves above wither. On the other hand, this method of applying heat does not cause withering and final drying nearly so quickly as steaming. There can be no doubt that the treated portions were killed by the hot wax. Microscopical examination indicates that the cells are dead, but that there is much less disorganization caused by this sort of treatment than by using steam. These stems do not show so much initial plugging of the lumina of the vessels, although the ducts finally become much discolored. As the table shows, leaves may remain turgid for a period of 5-23 days (or longer in case 5 cm. are killed), depending on the length of the stretch killed; while the maximum time of turgidity for stems with a section killed by steam did not exceed 18 days. To compare specific cases in table IV, nos. 14—S (1908), 50—S (1908), 5—S (1909), 24—S (1909), and 63—S (1910) each had 10 cm. treated; the leaves on these plants withered in 8 or 10 days. In table VII, nos. 3—W, 4—W, and 7—W each had the same distance killed, but the leaves did not dry until 14-34 days thereafter. They lasted nearly three times as long.

I have also determined the actual amount of water transpired by the leaves of a plant before and after treatment with the hot wax, just as was done in the case when steam was used (see tables V and VI). The average transpiration for each 24 hours for 5 days was determined, then 10 cm. of the stem were killed and the observation was continued. The results appear in tables VIII and IX. The daily loss in grams is shown in the second column in each table. Observations were made in order to compare the effect of temperature and weather conditions on the amount of transpiration. The average daily temperature was obtained, as before, by taking the average of the temperatures as recorded by the self-registering thermometer.

It will be noted that there is an increased amount of water transpired the first 2 days after treatment with the hot wax, although the temperature was lower than it was the first 2 days

before such treatment; there is also an increase on the fifth day over the fourth. In the case of stems with steamed sections no such increase occurs, as is shown by table VI. The steaming causes an immediate and continued falling off in the amount of water transpired. The plants used for the experiment, the results of which are tabulated in tables VIII and IX, were examined microscopically and tested with alkanin, and very little plugging of the lumina was found. No such discoloration of the parenchyma surrounding the bundles was observed as occurs in steamed stems.

TABLES VIII AND IX

SHOWING THE EFFECT ON DAILY TRANSPIRATION BEFORE AND AFTER KILLING 20 CM. OF THE STEM WITH WAX HEATED TO 110° C.

TABLE VIII—OBSERVATIONS BEFORE KILLING				TABLE IX—OBSERVATIONS AFTER KILLING				
Date 1910	Loss in grams	Average tem- perature	Weather conditions	Date 1910	Loss in grams	Average tem- perature	Weather conditions	Remarks
May 17	1.1	19° C.	Cloudy	May 22	1.9	19° C.	Clear	Plant in good condition
May 18	2.0	24° C.	Clear	May 23	2.6	20° C.	Cloudy	Plant in good condition
May 19	2.5	24° C.	Clear	May 24	1.8	21° C.	Cloudy	Plant in good condition
May 20	2.7	25° C.	Clear	May 25	1.4	26° C.	Cloudy	Plant in good condition
May 21	2.3	29° C.	Slightly cloudy	May 26	1.6	26° C.	Slightly cloudy	Leaf tips very slightly yellow
Average loss in 24 hours = 2.12 grams.				Average loss in 24 hours = 1.86 grams.				

The leaves also showed very little plasmolysis in the mesophyll cells, and the chloroplasts were in good condition. These results undoubtedly indicate that hot wax is superior to steam for killing the cells of stems without disarranging the tissues.

In view of SCHROEDER's observations, it will be instructive to examine again the results shown in table VI. After 10 cm. of the stem were steamed, a successive diminution in the amount of water lost in each 24 hours occurs. The leaves behave exactly as though they were wilting from lack of water supply, except that the process is not so rapid, owing probably to a certain amount of water being able to rise in the not completely plugged vessels. It is further

to be noted that after the second day the amount falls from 1.5 gm. to 0.9 gm., after which there is a more gradual daily diminution in the amount transpired. This seems to indicate, in the light of SCHROEDER'S results, that the leaves were dying, which is undoubtedly the case. Death is probably due to deleterious substances being introduced into the leaves from the killed portion of the stem. Examining table IX, in which the results are shown after using hot wax as a killing medium, we see that on the second day the plant increases the amount of water given off, which proves that it is not dying. There is also an increase on the fifth day over the fourth. I suspect that the leaves in this case have not been so severely poisoned as in the plant killed with steam.

That withering of the leaves on stems, which have been killed with heat, is not due to lack of water, but to the toxic action of substances which have been carried to the leaves, seems to be shown by the above-described experiments. The fact that the longer the heated region, the more rapid the leaves wither, seems to favor such a view. That leaves above a steamed or otherwise heated portion do not wither in the same way as those simply deprived of water, but often discolor before shriveling, also supports such a conclusion, as DIXON has already shown.

Histological examination of such leaves shows that the protoplasts and chloroplasts resemble those under diseased conditions more than those in leaves which are merely drying for lack of water supply. I agree with DIXON that leaves on cut branches die from lack of water supply, while in the case of leaves borne above a heated portion of the stem, they die because they dry.

THE UNIVERSITY OF WISCONSIN
MADISON

BRIEFER ARTICLES

ERGOT ON OATS

(WITH ONE FIGURE)

While harvesting the grain in the oat-breeding nursery conducted by the Office of Grain Investigations of the Department of Agriculture,



FIG. 1

in cooperation with the Iowa Agricultural Experiment Station, at Ames, Iowa, in July, 1909, a number of specimens of ergot (*Claviceps purpurea*) on oats were found. Ergot on oats is said to be quite common in Algeria, and probably occurs elsewhere, but a partial review of the literature does not show that it has been previously reported from the United States. The ergot masses which were found at Ames were in all cases near the base of the panicle, as shown in the accompanying illustration, and usually only one of the spikelets was affected. The disease was most common on the Burt oat, a variety which, strangely enough, is entirely resistant to smut. The season of 1909 was a particularly wet one, a

condition generally recognized as favorable to ergot epidemics. No occurrence of the disease was noted at Ames in the dry season of 1910. Specimens of ergot collected at Ames in 1909 are in the herbarium of the Iowa State College and in the pathological collection of the Bureau of Plant Industry, U.S. Dept. of Agriculture.—C. W. WARBURTON, Bureau of Plant Industry, U.S. Dept. of Agriculture.

CURRENT LITERATURE

BOOK REVIEWS

Researches on fungi

It might seem that the study of spore dispersal among the fungi offered little opportunity for important investigation, but the perusal of BULLER's recent volume on the subject shows how surprisingly little we really knew about the matter before he began his researches. The results of many years of patient investigation are now brought together in an elaborate manner, and it is safe to say that only once in a while is it possible to find a volume which contains so much that is new to botanists.¹ One hardly knows whether to admire most the many new contributions, the ingenious mechanical contrivances which made the contributions possible, or the limitless patience which Professor BULLER has shown in working out the uttermost details of his subject. Although some of the results here given have been published in various papers, no attempt will be made in this review to distinguish between such results and those given for the first time, though most come under the latter head.

After some chapters which review the chief features of the reproductive organs of the Hymenomycetes, BULLER gives an account of his experiments which show that the fruiting bodies of these plants are "adjusted" in a most remarkable manner to spore dispersal. In the first place, the apogeotropic stipes exhibit the swaying movements that are so familiar in the shoots of seed plants; in one case there was noted a curvature through an arc of 90° in 18 minutes. It is shown also that the gills exhibit geotropic reactions. As a result of the geotropic curvatures of the stipe, and of the gills, the latter are strictly vertical when in a state of equilibrium; the great advantage of such reactions is that they permit the fall of the spores between the gills (or through the tubes in the case of the polypores). In some cases, but not in all, light as well as gravity stimulates stipe curvatures. Careful estimates are made of the number of spores and of their rate of fall in various fruit-bodies, and although everyone knows that the spores are very numerous, the numbers given by BULLER seem almost unbelievable. For example, in a fruit of *Agaricus campestris* there were estimated to be 1,800,000,000 spores, and as they took two days to shed, they dispersed at the rate of 40,000,000 per hour. In

¹ BULLER, A. H. REGINALD, Researches on fungi; an account of the production, liberation, and dispersion of the spores of Hymenomycetes treated botanically and physically. Medium 8vo. pp. xi+287. pls. 5. figs. 83. London, New York, Bombay, and Calcutta: Longmans, Green and Co., 1909. 12s. 6d.

Coprinus comatus there were estimated to be 5,240,000,000 spores, which fell at the rate of 100,000,000 per hour; these spores have an average length of $12.55\ \mu$, so that if they were arranged end to end, the spores of a single *Coprinus* fruit would extend a distance of 41 miles. Probably the most productive of all plants is the giant puffball, *Lycoperdon giganteum*; in a fruit whose dimensions were 40 cm. $\times$ 28 cm. $\times$ 20 cm. there were estimated to be seven trillion spores. The advantage of having such enormous numbers of spores is evident, when it is realized that in *Polyporus squamosus*, for example, it is estimated that only about one spore in a trillion is able to develop into a plant.

The most important contributions of the volume concern the fall of the spores. Ordinarily, spore fall cannot be observed by the naked eye, even though the spores are discharged at the rate of a million a minute, but Professor BULLER has shown that by the use of a concentrated beam of light, it is possible to observe the fall without the use of magnification. By this means there was made the surprising discovery that in the more xerophytic species, with leathery fruit bodies, vitality is retained for a number of years; specimens may be dried and moistened many times, each moistening resulting in a renewal of spore dispersal. In such forms it is obvious that the fruit bodies may be collected and spore discharge studied at leisure. In two cases it was shown that the spores of fungi that had been kept dry for three years still retained a capacity for germination. By the use of ingenious methods devised by the author, the rate of spore discharge, which is so rapid as to be incapable of observation by the microscope, was calculated with mathematical precision. In *Amanita vaginata* the spores are shot out horizontally with an initial velocity of 400 mm. per second, but so rapidly does the rate slow down on account of friction with the air, that when they have reached a distance of 2 mm. from their original position, they begin to descend. The terminal falling velocity of a moist spore is about 5 mm. per second, and is reached in 0.04 second. The trajectory described by the spore is somewhat unique in that it passes so sharply from horizontality to verticality, and to such a trajectory BULLER gives the name *sporabola*. In connection with these studies it is interesting to note that the author has made the first test of the applicability of STOKES'S law to the fall of microscopic spheres in air.

The mechanism of spore discharge receives attention, but is not certainly demonstrated, though it is shown that the spores are not squirted out by the bursting of the sterigmata under hydrostatic pressure. The author thinks that discharge is due to the rupture of lateral walls at the junction of the sterigma and the spore through the influence of endosmotic pressure. BULLER points out that the trajectory of the spore is admirably suited for effective spore discharge, for if the spores shot out much less than 2 mm. they might not be fully freed from the gill whence they come, while if they shot out farther, they might be in danger of hitting the opposite gill. BULLER appears also to have solved the question as to the advantage of deliquescence in *Coprinus*.

It used to be supposed that insects crawling through the deliquescent portion aid in scattering spores, but it is found that the spores discharge before the pileus deliquesces; deliquescence, however, removes the older part of the pileus from beneath the parts where active shedding is taking place, thus making a cylindrical pileus as well adapted for spore dispersal by currents as is a horizontal pileus. Hence the author regards *Coprinus* as a more specialized form than one like *Agaricus*. The closing chapters deal with spore dispersal in the Ascomycetes and in *Pilobolus*.—HENRY C. COWLES.

The Chicago textbook

It has been many a day since any botanical-educational work has been anticipated with such interest as the book before us. Entirely new: prepared by three sympathetic co-workers, all eminent both as investigators and teachers: elaborated under the facilities and freedom provided by one of our most progressive universities: the appearance of such a work is naturally an educational event. The result, in greater part, is now before us,^{1a} and the remainder is promised for the very near future.

Of the three parts, part I, of 296 pages, is Morphology, by Professor COULTER. It is devoted wholly to the description and illustration of the natural groups from Thallophytes to Spermatophytes, the axial idea of the treatment being the morphological evolution of structures. The title Morphology, therefore, is to be read as Special rather than General Morphology. There will be, I believe, but one opinion upon these pages; that they are a model of precise, expressive, well-balanced description. Throughout the work runs the evidence of advanced knowledge combined with a spirit of caution and an emphasis upon the study of things as they are rather than as they should be. If there is anywhere a better account of the groups, and of the morphological evolution, of plants, it is not known to the present reviewer; and it will take a more intensive knowledge of these subjects than he possesses to detect any material fault or error therein. The illustrations, no less than 618 in number, are almost wholly new to textbooks, though they are largely taken from special works of the author or his students, a fact which will explain the frequent larger size and greater elaboration of detail than would otherwise be selected for such a work. There is not, of course, much room for anything strikingly new or suggestive in the treatment of the subject, but most readers, no doubt, will turn with especial interest to the discussion of the "new anatomy"; and there will be general relief to find that it differs much less from the old than we had perhaps been led to expect.

Part II is Physiology, by the late Professor Barnes, and we cannot but consider it a piece of singular good fortune that he was able to complete this embodiment of his extensive knowledge and teaching skill before his lamented

^{1a}COULTER, BARNES, and COWLES, A textbook of botany. Vol. I. Morphology and physiology. 8vo. viii+484 pp. figs. 699. New York: American Book Company. 1910. \$2.00.

death. In fine qualities of exposition and balance this part is a worthy companion of the first. In places, however, it suffers a little from an extreme of condensation, although its 189 pages (with their 81 illustrations) would seem to be ample for the subject in comparison with part I. Thus the treatment of capillarity (pp. 314, 349) and of osmotic phenomena (p. 309) is too brief for complete clearness. And (while we are faultfinding) the inference (p. 371) as to the wastefulness of the plant motor does not follow from the evidence; and surely the protoplast is not dragged, but pushed, from the wall (p. 310), and it is settled that the products of decomposition of chlorophyllin have nothing to do with reddening the leaves (p. 368). But it is upon such trifles as these that the fiendish glee of the reviewer in the detection of error must glut itself in this book, and their very insignificance is eloquent testimony to the general accuracy and worth of the work, which offers an unsurpassed synopsis of the present state of our knowledge of plant physiology.

This part, and in lesser degree the first, reflects the efforts of the authors to give more exact definition to terminology, especially in the direction of elimination of teleological expressions. The result is, however, not always happy, and it is a question whether it is not better in most cases to retain the familiar and expressive, even though teleological and animistic, terminology, giving frequent warning to the student as to its scientifically erroneous character.

Every teacher will wish to know to what grade of instruction the work is adapted. Presumably part III will correspond in this respect to those before us. The title shows that it is intended "for colleges and universities." If by colleges is meant the general elementary courses in which botany is presented for the first time to undergraduates, then in the opinion of the reviewer the book contains too much, and is of too advanced a character, unless the plan is followed of irrigating the student mind with a vast flood of information in the hope that out of the profusion he will find and retain something that interests him. But for the second courses in colleges, those devoted to morphology, physiology, and ecology in particular, the work seems to the reviewer wholly admirable, and much better adapted than any other to the needs of American college students and our methods of instruction. For this purpose, however, the parts should be obtainable separately, and the physiology would have borne some amplification.

The book is beautifully printed, and the excellent illustrations are admirably reproduced. Altogether it is mechanically, as it is in substance, one of the most attractive of textbooks.—W. F. GANONG.

Lichens of Minnesota

Professor BRUCE FINK has been studying the lichens of Minnesota since 1896, and the result has appeared in the form of a large bulletin from the U.S. National Museum.² It is a notable contribution to the lichenology of North

² FINK, BRUCE, The lichens of Minnesota. Contrib. U.S. Nat. Herb. 14: pt. 1. pp. xvii+269. pls. 51. figs. 18. 1910.

America, for although it includes only the forms of a single state, the peculiarly wide distribution of species of lichens makes the bulletin really a manual for the determination of the lichens of the whole country. The bulk of the bulletin consists of the catalogue of species, but it is much more than that, for the species are described with a fullness and an exactness unusual in such descriptions, and convenient keys make the approach to genera and species seem simple enough. The numerous admirable reproductions of photographs also bring clearly to the student the field aspect of the different forms.

There are 68 genera presented, comprising 314 species, and under the species there are often numerous varieties. It is of interest to note that the genera are not large, only 6 of them comprising 10 or more species, and the 2 largest (*Lecidea* and *Cladonia*) comprising only 29 species each. This means that the remaining genera are represented on the average by about 3 species. This is a striking illustration either of the constancy of lichen species over wide areas, or of the caution of lichenologists in recognizing variations as species. This is perhaps further emphasized by the fact that in the present publication not a single new species is proposed.

The catalogue is preceded by a general account of lichens, so that the student of classification may obtain adequate information as to the morphology of the group. There are also some interesting paragraphs dealing with the economic rôle of lichens, under the following heads: "as purifiers of the air," "as aids in rock disintegration," "as food," "as medicinal agents," "as dyestuffs," and "as related to the welfare of trees."

This book should prove a great stimulus to the study of lichens, a group which deserves to be more cultivated by American botanists.—J. M. C.

MINOR NOTICES

Plant-breeding in the United States.—Professors v. RÜMKER and v. TSCHERMAK have published a report³ of their extended American visit during the spring and summer of 1909. The writers inspected most of the institutions in which either theoretical studies in genetics, or practical experiments in plant and animal breeding are in progress, as well as the work of numerous private breeders. The whole report forms an exceedingly keen and accurate review of the present operations along these lines in America. The material has been well sifted, analyzed, and systematically arranged. The chapters close with full bibliographies. In the first part, which is occupied with American studies in genetic theory, full reviews are given of the newer work of SHULL, CASTLE, TOWER, MORGAN, MACDOUGAL, and others. Part II, dealing with practical breeding operations, begins with an extended discussion of American experiment station investigations in corn breeding. The long-continued experiments at the Illinois station on the

³ RÜMKER, v., and TSCHERMAK, v., *Landwirtschaftliche Studien in Nord-Amerika, mit besonderer Berücksichtigung der Pflanzenzüchtung*. pp. 150. Berlin: Paul Parey. 1910.

improvement of certain economic characters in corn by continuous selection, are given careful consideration, as also the theoretically more important work of SHULL and EAST. Full accounts of the experiments in breeding other cereals and various fodder plants under way at several experiment stations follow. The writers furnish what is perhaps the best brief general critique of LUTHER BURBANK and his much be-written work that has yet appeared, and which affords a refreshing change from the usual reiterated adoration of the stoneless prune, the plumcot, and the spineless cactus, to which our ears have so long been accustomed. What is still more interesting is the very appreciative and much deserved commentary on the valuable work of HANSEN in the amelioration of the wild fruits of the northwest plains region. The authors have been at pains to grasp thoroughly and put down minutely the rather complex morphology of our national Department of Agriculture and its protean subdivisions, accompanied by an astonishing genealogical tree of its ramifying functions and personnel that is worth that department's while to reproduce in English. The independent agricultural colleges visited were those of Kansas, South Dakota, and New Jersey, and those with university affiliations were Cornell, Wisconsin, Illinois, Minnesota, Nebraska, California, and Arizona, the organization and equipment being noted in each case. Agronomic methods, soil culture, and agricultural economics in general are reviewed so far as the writers had time and opportunity to observe. Full and detailed accounts occur of the apparatus in use at the various experiment stations and botanical institutes visited. The authors display throughout a well balanced judicial temper in comparing American and European conditions as regards agricultural education and experimental work. The *Pracht* and *Glanz* of some of our munificently endowed American scientific and educational institutions do not conceal from the acute vision of the authors of this *Bericht* the humiliating circumstances that too often afflict the occupants of their chairs. Meager salaries, incessant teaching, papers and publications issued under forced draft, and the precious requirements of our American red-tape technique, which call for the perpetual pumping out of reports of scientific progress up to Saturday night, all of this has not escaped the European commentators' attention. "Dabei ist es jedoch noch immer als ein schwerer Fehler zu bezeichnen, dass die amerikanischen Mäzene zwar der Wissenschaft mit Recht herrliche Paläste bauen, die Diener der Wissenschaft jedoch—die Professoren und Dozenten—regelmässig vergessen" (p. 150).—H. F. ROBERTS.

Experiments in plant physiology.—HEALD and LEWIS have published⁴ a set of experiments in plant physiology, designed to form the basis for a year of university work. The experiments are grouped under four heads arranged in the following order: growth (exps. 1-15), movement of water and gases (exps. 16-61), nutrition (exps. 62-115), and irritability (exps. 116-150). The

⁴ HEALD, F. DEF., and LEWIS, I. M., Experiments in plant physiology. pp. 70. figs. 24. Austin, Texas: the authors. 1910.

authors apparently feel it desirable to teach as many facts as possible through demonstration or experiment. This probably accounts for the large number of experiments used for the year's course, and for their qualitative and in many cases extremely elementary character. The experiments stand quite in contrast with the aims set forth by GANONG in his manual for a college course in this subject. "The emphasis is thrown, for advanced or college work, not upon qualitative results obtained by students from apparatus of their own making, but upon quantitative results obtained from practically accurate or normal apparatus manufactured expressly for its particular use." The lack of reliability in much of the data of plant physiology is due to the loose qualitative methods used in the subject. I know no better place to begin the development of reliable quantitative technique than in college and university courses. GANONG has repeatedly urged this necessity. Time-honored experiments that have taught misconceptions ought to be dropped from manuals or modified so as to teach the truth. As an illustration, we may mention the use of the potassium bichromate and ammoniacal copper sulphate screens for the purpose of determining the relative photosynthetic value of red and blue light. KNIEP and MINDER⁵ have shown that the results obtained in this case are due to different intensities and not to different qualities of the light. This experiment is of significance only when the screens are so arranged as to give equal energy values. Under this condition KNIEP and MINDER found equal photosynthetic activity for the two ends. When exact chemical methods give more trustworthy results (as is the case in experiment 35 on the retention of salts by soil), one can hardly see why they should be avoided in a university course.—WILLIAM CROCKER.

Outlines of geologic history.—Under this title a series of essays involving a discussion of geologic correlation is published.⁶ The essays were presented before Section E at the Baltimore meeting (1908) of the American Association, and include three of interest to botanists: "The upper paleozoic floras, their succession and range," by DAVID WHITE; "Succession and range of mesozoic and tertiary floras," by F. H. KNOWLTON; "Origination of self-generating matter and the influence of aridity upon its evolutionary development," by D. T. MACDOUGAL. The first two papers cited present in convenient outline form the succession of floras from the middle Devonian to the end of the Tertiary. Naturally the presentation is chiefly stratigraphic, with suggestions as to climatic changes; but the material for a consideration of the historical basis for phylogenetic conclusions is thus made more available. MACDOUGAL's essay, as the title suggests, is highly speculative, but the basis of facts which

⁵ BOT. GAZETTE 49:390. 1910.

⁶ Outlines of geologic history with especial reference to North America. Symposium organized by BAILEY WILLIS. Compilation edited by ROLLIN D. SALISBURY. Chicago: The University of Chicago Press. 1910. \$1.50.

underlies the discussion has been developed by his physiological investigations, chiefly in connection with the vegetation of arid areas.—J. M. C.

Scientific expedition to New Guinea.—A second part of volume VIII, continuing the account of the botanical results of this expedition, has been published recently,⁷ which includes about 50 families of the higher plants, over 190 genera, and approximately 300 species and varieties. The taxonomic work has been done by noted specialists, and their results have been ably edited by Dr. H. A. LORENTZ. Nearly one-third of the species and varieties enumerated are new to science, and the following genera are published here for the first time: *Salacicatea* of the Hippocrateaceae, *Diandriella* of the Araceae, and *Cyrtandropsis* of the Gesneriaceae. The more important constituents of the flora, as shown by families, are: the Euphorbiaceae (60 species), Leguminosae (52), Piperaceae (21), Araceae (20), Myrtaceae (19), and Compositae (17). The publication is a scientifically important contribution to our knowledge of the flora of New Guinea.—J. M. GREENMAN.

NOTES FOR STUDENTS

Current taxonomic literature.—O. AMES (*Torreyia* 10:90, 91. 1910) records a new species of *Ponthieva* (*P. Brittonae*) from the Bahamas.—J. C. ARTHUR (*Mycologia* 2:213–240. 1910) under the title "Cultures of Uredineae in 1909" has placed on record some of the results of his researches during the past year, and includes two new species of *Gymnosporangium* described by F. D. KERN.—W. BECKER (*Beih. Bot. Centralbl.* 26:289–390. 1910) has issued the second and closing article on the taxonomy of European violets, embodying the results of long-continued study in this genus.—M. BOULY de LESDAIN (*Bull. Soc. Bot. Fr.* IV. 10:236–240. 1910) under the title "Notes lichénologiques no. XII" has described several new species of lichens, some of which are from Mexico.—T. S. BRANDEGEE (*Univ. Calif. Pub. Bot.* 4:85–95. 1910) has published 23 new species of flowering plants from Mexico; the paper is based chiefly on collections made in the state of Puebla by C. A. PURPUS, and the types are deposited in the herbarium of the University of California. One new genus (*Amphorella*) of the Asclepiadaceae is proposed.—N. L. BRITTON (*Bull. Torr. Bot. Club* 37:345–363. 1910) in continuation of his studies on West Indian plants presents a synoptical treatment of the genus *Comocladia*, recognizing 18 species of which 7 are indicated as new to science; the article includes also descriptions of 24 new species of spermatophytes belonging to different genera.—G. DISMIER (*Bull. Soc. Bot. Fr.* IV. 10:Mém. 17, pp. 1–37. 1910) under the title "Revision des Philonotis de l'Amérique" recognizes 25 species, 2 of which and several varieties are new.—P. DUSÉN

⁷ Nova Guinea. Résultats de l'expédition scientifique Néerlandaise à la Nouvelle-Guinée en 1907 sous les auspices du Dr. H. A. LORENTZ. Vol. VIII, Botanique Livraison II. 4to, pp. 221–426. pls. 52–68. Leide: E. J. Brill. 1910.

(Arkiv för Botanik 9:no. 5, pp. 1-50. *pl.* 1. 1910) under the title "Beiträge zur flora des Itatiaia" has published 4 new species of flowering plants; the same author (*ibid.* no. 15, pp. 1-37. *pls.* 1-8. 1910), in cooperation with the well known specialists H. CHRIST, E. HÄCKEL, and A. COGNIAUX, has published 25 new species and 3 varieties of vascular plants from Paraná, southern Brazil. The types are mostly in the government museum at Stockholm.—E. L. EKMAN (*ibid.* no. 4, pp. 1-56. 1910) records the results of a botanical expedition to Argentina and includes descriptions of several new species and varieties of Malvaceae and Sterculiaceae.—A. D. E. ELMER (Leaf. Phil. Bot. 2:659-701. 1910) in continuation of studies on the flora of the Philippines has described 10 new species of the Myrsinaceae, 3 new species and a new genus (*Whitfordia*) of the Leguminosae, and 10 new species belonging to different families of flowering plants. J. GILLET and E. PÂQUE (Ann. Mus. Congo. Botanique Sér. V. fasc. 1. pp. ix+120. 1910) in a series of publications by the Belgian government on the flora of the Congo have issued recently a very interesting contribution entitled "Plantes principales de la région de Kisantu." The paper gives the native and scientific names of plants as well as their uses, and is illustrated with over twenty photographic illustrations.—E. L. GREENE (Leaf. Bot. Obs. & Crit. 2:105-120. 1910) describes 25 new species of flowering plants mostly from western United States and northern Mexico; of these 12 belong to the genus *Morus* and are related to *M. microphylla* Buckley.—F. D. HEALD and F. A. WOLF (Mycologia 2:205-211. *pl.* 31. 1910) have published a new genus (*Cyanospora*), referred to the Ceratostomaceae; the fungus is associated with the whitened areas on the trunk and branches of the mountain cedar of western Texas and northern Mexico and is thought to be parasitic.—G. G. HEDGCOCK (*ibid.* 155, 156) records a new polypore (*Polyporus amarus*), found on living trunks of *Libocedrus decurrens*; it is said to be the cause of "pin-rot" or "peckiness" of the heartwood of these trees.—A. A. HELLER (Muhlenbergia 6:81, 82. 1910) under the title "The North American Lupines II" describes a new species of *Lupinus* (*L. silvicola*) from California.—G. KOIDZUMI (Journ. Sci. Coll. Univ. Tokyo 27:1-128. *pls.* 1-3. 1910) gives a list of plants collected on the Japanese part of the Island of Sachalin by Mr. G. NAKAHARA in 1906. The list comprises some 200 genera and about 300 species, many of which have not been recorded hitherto from this region.—H. KYLIN (Sv. Bot. Tidsk. 4:146-149. *pl.* 6. 1910) describes and illustrates a new species of *Batrachospermum* (*B. Skottsbergii*) from Tierra-del-Fuego.—W. A. MURRILL (Mycologia 2:248. 1910) has published a new species of *Ceratomyces* (*C. jalapensis*) from the vicinity of Jalapa, Mexico.—TH. LOESENER (Verh. Bot. Ver. Prov. Brandb. 51:1-36 [179-214]. 1909-1910), in collaboration with different specialists, gives an annotated list of plants collected in Mexico and Central America by C. and E. SELER. The paper is the sixth in the series of *Plantae Selerianae* and includes descriptions of 11 new species and 2 new varieties of flowering plants.—G. E. OSTERHOUT (Muhlenbergia 6:46, 47. 1910) describes a new species of *Aulospermum* (*A. Betheli*), a

new variety of *Aster laevis*, and one of *Arnica Parryi* from Colorado.—F. PETRAK (Bull. Soc. Bot. Genève II. 2:167-171. 1910) has published a new genus (*Wettsteinia*) of Compositae, based on *Carduus nidulans* Ruprecht.—E. P. PHILLIPS (Kew Bull. 286-290. 1910) has characterized a new genus (*Spatallopsis*) of the Proteaceae; the genus is a segregate from *Spatalla*, differing principally in having a regular calyx and conical stigma and, as present understood, contains 5 species, all of south African distribution.—L. QUEHL (Monats. für Kakteenkunde 20:139, 140. 1910) describes and illustrates a new species of *Mamillaria* (*M. Emskötteriana*) from Mexico.—J. F. ROCK (Bull. Torr. Bot. Club 37:297-304. 1910) has published 4 new species of flowering plants from Hawaii.—P. A. RYDBERG (*ibid.* 313-335, 443-471) in continuation of his "Studies on the Rocky Mountain flora" has described several new species of Compositae.—V. SCHIFFNER (Oesterr. Bot. Zeitschr. 60:169-173. 1910) presents a consideration of the genus *Chiloscyphus*, segregating therefrom a group of species for which he proposes the new generic name *Heteroscyphus*.—R. SCHLECHTER (Rep. Nov. Sp. 8:453-458. 1910) has published several new species of Orchidaceae, of which 7 are from Central and South America.—J. K. SMALL (Torreya 10:186-188. 1910) describes a new genus (*Carteria*) of the Orchidaceae; the plant is a native on the Everglade Keys, Florida, and is also said to occur in the Bahamas.—D. R. SUMSTINE (Mycologia 2:125-154. 1910) under the title "The North American Mucorales I" gives a synoptical treatment of the group with keys to the genera and species.—F. THEISSEN (Broteria Ser. Bot. 9:5-44. 1910) under the title "Perisporiales Riograndenses" gives an annotated list of the Perisporiaceae of southern Brazil, including several species new to science; the list is supplemented by a catalogue of the host plants.—C. TORREND (*ibid.* 45-53) presents the results of studies on the Myxomycetes of Portugal and proposes a new genus (*Helolachnum*) of the Discomycetes.—P. WILSON (Bull. Torr. Bot. Club 37:437, 438. 1910) has described a new species of *Ravenia* and one of *Spathelia* from eastern Cuba.—F. A. WOLF (Mycologia 2:241, 242. pl. 32. 1910) has published a new species of *Macrophoma*; the fungus is parasitic on leaves of the American mistletoe (*Phoradendron flavescens*), and up to the present time has been found only in Texas.—H. WOLFF (Rep. Nov. Sp. 8:414, 415. 1910) has published two new species of *Eryngium*, namely *E. Ekmanii* from Argentina and *E. Harmsianum* from California.—Several authors (Kew Bull. 192-197. 1910) have described new species of flowering plants, including a new *Tabebuia* (*T. stenocalyx*) from Trinidad and a *Catopsis* (*C. penduliflora*) from Peru.—J. M. GREENMAN.

Russian grain rusts.—During a number of years JACZEWSKI has made a study of the grain rusts in Russia, the results of which have been published in a Russian monograph. Believing that local observations in different regions may serve to elucidate some phases in the life history of the rusts, the author has made those results of his studies which might be of general interest avail-

able to a wider group of readers by publishing an abridged account in German.⁸ While the paper contains little that is essentially new, it gives an excellent account of the biology of the collective species *Puccinia graminis* as observed by the author in Russia. The account is valuable for comparison with similar observations made in other regions, for it is possible that the ecological and biological routine of development of the grain rusts is not the same in all regions. An illustration of this possibility is found in the present paper in reference to the different sources of infection of new grain in spring in Russia and in the United States.

JACZEWSKI attributes the primary infection of wheat in spring entirely to aecidiospores from barberry. In the plains of the middle west, where barberry bushes are rare or do not occur at all over rust areas, both BOLLEY and CARLETON have found that the fungus is carried through the winter by means of surviving uredospores. In Russia JACZEWSKI finds that none of the uredospores survive through the winter, either on the straw or on living plants; nor does the mycelium of the fall survive on seedling wheat, for when infected seedlings are covered with glass cases they remain free from rust the following summer. These experiments, as well as some similar ones with older rhizomes of wheat and orchard grass, the author regards as disproving the validity of ERIKSSON's mycoplasma theory.

As to the spermatia, the author differs from the usual cytological interpretation of considering them as male cells, and considers them to be of the nature of conidia. It must be admitted that there is as much evidence for one view as for the other. Their persistency and universal occurrence he thinks is an objection to regarding them as functionless organs.

Of particular interest is the long series of cultures of uredospores on different grasses. The results are tabulated in a manner easily comprehended. A comparison of his own results with those of others suggests the possibility that the degree of specialization of form-species of rusts to certain hosts may not be the same for all regions, but may depend upon local conditions.—H. HASSELBRING.

Lipoids and respiration.—By extracting wheat germs with various solvents of lipoids, and then determining the carbon dioxid evolved from the germs during a given period of time, PALLADIN and STANEWITSCH⁹ seek to establish a relation between respiratory activity and the lipoid content of plants. The germs were extracted with a given solvent until nothing was removed by new quantities of the solvent. The solvent was then removed and the germs were placed on filter paper and soaked in water for 30 minutes, after which they

⁸ JACZEWSKI, A. VON, Studien über das Verhalten des Schwarzröstes des Getreides in Russland. Zeitschr. Pflanzenkrank. 20:321-359. figs. 8. 1910.

⁹ PALLADIN, W., and STANEWITSCH, E., Die Abhängigkeit der Pflanzenatmung von den Lipoiden. Biochem. Zeitschr. 26:351-369. 1910.

were put into a U-tube with the filter paper on which they had been soaked. Air was drawn through the apparatus for 30 minutes, after which the carbon dioxid was determined at 3-hour intervals for a period of 9 hours in most of the experiments. The solvents used in the different experiments were alcohol, ether, anilin, chloroform, ethyl acetate, turpentine, benzine, olive oil, acetone, benzene, and toluene.

In each case two parallel experiments were conducted, one with toluene vapor drawn through the tube, and one without. In the first experiment in which living germs were used they were found rotted at the end of the 9-hour period in the tube without toluene. In the other cases it was found that the amount of carbon dioxid evolved varied according to the solvent with which the germs had been extracted. The order arranged according to the intensity of depression is as follows: alcohol, ethyl acetate, ether, benzine, chloroform, aniline, turpentine, olive oil, benzene, acetone, toluene. In the tubes with toluene this sequence is different, but the toluene vapor in every case caused a depression of the amount of carbon dioxid evolved. The authors point out that there is a general relation between the quantity of lipoids dissolved by acetone, benzene, chloroform, ether, and alcohol, and the depressing effect of these substances on respiration. There is, however, no strict proportionality between the quantity of lipoids removed and the depression of respiration, as would be expected if the depression were due only to the removal of lipoids and not to other possible effects of the solvents.—H. HASSELBRING.

Germination.—GASSNER¹⁰ has studied the germination characters of seeds of two South American grasses, *Chloris ciliata* and *C. distachophylla*. The behavior of the two species is in the main the same, so we need consider only the results with *C. ciliata*, on which the main work was done. With dry storage the seeds show a marked after-ripening. The most favorable period of dry storage is 30–40 weeks. With 10 weeks or less of dry storage none will germinate in darkness at optimum temperature, but after 39 weeks 7–8 per cent will germinate under the same conditions. After 9 weeks of dry storage, only 3 per cent germinate in light, but after 39 weeks 73 per cent respond under the same conditions. If the germinators are dark during the early periods of germination and then transferred to light, the early subjection to darkness greatly reduces the total percentage of germination; the seeds become “dunkelharten.” This effect of darkness appears only when the temperature is above the minimum for germination (20° C.). At low temperatures (6–10° C.) the germination is not affected by such a period of darkness. GASSNER lines the experimental facts up with the conditions the seed must meet in nature, which gives great ecological significance to his results. Whatever the ecological value of such work, it must be stated that it adds little to a funda-

¹⁰ GASSNER, GUSTAV, Ueber Keimungsbedingungen einiger südamerikanischer Gramineensamen. Ber. Deutsch. Bot. Gesell. 28:350–364. 1910.

mental knowledge of delayed germination. From the physiological side we need to know the structures producing the delay, and how they are acted upon by the various conditions that will shorten it. GASSNER mentions two classes of seeds favored in their germination by light: the "dunkelharten" type, *C. ciliata* and *Ranunculus sceleratus*; and those that are not affected by a period of darkness, *Poa* and many others.—WILLIAM CROCKER.

Osmotic pressure of leaves.—DIXON and ATKINS¹¹ have devised a thermo-electric method for determining the freezing points of juices of plants. The advantage of the apparatus over BECKMANN'S lies in the fact that the determination can be made with 2.5-5 cc. of liquid instead of 12 cc. or more. The apparatus was used for determining the osmotic pressures of the sap of foliage leaves. The osmotic pressure varied with different species and individuals under the same conditions, but was constant for an individual under a given condition. In an individual of *Syringa vulgaris*, change of condition brought about a change in pressure from 24.58 to 11.58 atmospheres. The amount of pressure was not determined by the height of the leaves above the ground, nor by the resistance of the conducting tracts supplying the leaves, but in every case the osmotic pressure was much greater than the tension of the water supply could have been. Variations were attributed in the main to variations in carbohydrate and water content. The osmotic pressure of leaves increased with insolation, loss of water, and age. The highest osmotic pressure found for *Syringa vulgaris* was 26.87 atmospheres. The authors believe that during summer, when sugars are abundant and transpiration great, leaves of *Syringa* may develop a pressure as high as 30-40 atmospheres. The high pressures of leaves is quite in contrast to the pressures of roots of the same species. The pressures in the roots varies from 4 to 6 atmospheres. These data of course furnish support for the cohesion theory of rise of sap. One wonders how closely the osmotic pressure of extracted juices corresponds to that of the living cells.—WILLIAM CROCKER.

Oxidation of hydrogen by microorganisms.—NIKLEWSKI'S¹² full report of work, which has been intermittently in progress since 1904, makes an interesting and valuable contribution. The study includes the isolation of two species of rod bacteria which are both morphologically and physiologically distinguishable. Neither of the two species isolated can develop in an oxyhydrogen atmosphere without the company of the other, but when both are present under suitable conditions for growth a condensation of the oxyhydrogen gas occurs. If an inorganic nutrient medium is inoculated with

¹¹ DIXON, H. H., and ATKINS, W. R. G., On osmotic pressures in plants; and on a thermo-electric method of determining freezing points. Sci. Proc. Roy. Soc. Dublin N.S. 12:275-311. 1910.

¹² NIKLEWSKI, BRONISLAW, Ueber die Wasserstoffoxydation durch Mikroorganismen. Jahrb. Wiss. Bot. 48:113-142. 1910.

ordinary soil and surrounded by an oxyhydrogen atmosphere containing some carbonic acid, a film will develop which represents the growth of the two species of *Hydrogenomonas*, *vitrea* and *flava*. Through the mutual activity of those two species of bacteria constituting the film, the carbonic acid is reduced and hydrogen is oxidized. Each of those organisms is capable of heterotropic feeding, but *vitrea* is unable to develop upon a series of substances which afford suitable food for *flava*. The reason why neither organism can alone develop in the oxyhydrogen atmosphere is that it cannot endure the high tension of the oxygen, for which limit for injurious effect is close to 53 mm. pressure. Free hydrogen is more or less protected against oxidation by those organisms by organic substances which have a food value for them. The author ventures the opinion that in the presence of carbonic acid the hydrogen is used to form compounds with the carbonic acid which are in turn oxidized.—RAYMOND H. POND.

Reduction.—ZALESKI¹³ makes a study of the reduction processes in plants. A brief review of the literature on the subject is followed by a number of experiments. Methylene blue was used as the agent to be reduced. He finds a parallel between the reduction activity and alcoholic fermentation. The main evidence of such a parallel is shown by the fact that various acids, bases, and salts affect similarly the two processes, and plant organs in general show the two processes in a like degree. He points out the fact that we do not know the agent that causes such reductions. It may be an enzyme, reductase or hydrogenase, or it may be a chemical compound capable of absorbing oxygen. One quickly sees the need of a master mind in this field, a person who can use exact chemical methods rather than haphazard ones.

KORSAKOW¹⁴ finds that sodium selenate stops the action of zymase in killed yeast—"zymin"; while it greatly increases its activity in living yeast. This agrees with the effect PALLADIN¹⁵ found that ether and other poisons had on CO₂ (respiratory) production in higher plants. While the selenate stopped the fermentative activity of the dead yeast, it did not modify its reductive power, as shown by the deposit of selenium. Hence it is argued that the two processes are independent, in contrast to ZALESKI's contention.—WILLIAM CROCKER.

Evaporation in marsh vegetation.—Investigating the atmospheric factors in herbaceous marsh vegetation by means of thermometers and a modification of the porous cup atmometer, YAPP¹⁶ demonstrated a marked stratification in

¹³ ZALESKI, W., Ueber die Rolle der Reduktionprozesse bei der Atmung der Pflanzen. Ber. Deutsch. Bot. Gesell. 28:319-329. 1910.

¹⁴ KORSAKOW, MARIE, Ueber die Wirkung des Natriumselents auf die Ausscheidung der Kohlensäure lebender und abgetoteter Hefe. Ber. Deutsch. Bot. Gesell. 28:334-338. 1910.

¹⁵ PALLADIN, W., Zur Physiologie der Lipoide. Ber. Deutsch. Bot. Gesell. 28:120-125. 1910.

¹⁶ YAPP, R. H., On stratification in the vegetation of a marsh and its relation to evaporation and temperature. Annals of Botany 23:275-320. 1909.

the vegetation with different conditions in the different strata. In vegetation with an average height of five feet, the average rate of evaporation above the herbage, about the middle of it, and in the lower strata, was according to the ratios 100:32.8:6.6. Similar vegetation about two feet high gave corresponding ratios of 100:56.2:14.7. These ratios are valuable indications of comparative humidity within the vegetation and upon its surface. Temperature readings showed that the upper layers of the vegetation were exposed to a greater daily range of temperature than either the free air above or the lower layers of the vegetation. As the different species vary much in their average height, it will be seen that few species of plants forming the marsh vegetation have to face precisely the same set of physiological conditions, hence xerophytic and non-xerophytic marsh plants may grow side by side, each in the different conditions suited to its requirements.—GEO. D. FULLER.

Catalase.—ROSENBERG¹⁷ attempts to settle the question whether catalase belongs to the anaerobic or aerobic respiratory enzymes. She finds it in great abundance in seeds and seedlings showing low anaerobic and high aerobic respiration. In yeast it decreases with fermentative activity. In seeds it increases as germination progresses. Acids and most salts markedly diminish its activity, while 0.5 per cent Na_2HPO_4 and K_2HPO_4 and 0.25 per cent Na_2CO_3 greatly increase it. From these facts she concludes that catalase belongs to the aerobic respiratory enzymes. There are two serious criticisms that must be offered against the work. The destructive effect of acids on catalase and the rapid development of such acids in dead plant tissues is well established. Her methods apparently entirely overlooked these facts. It is probable, therefore, that she was measuring only a fraction of the entire catalase, and therefore that her determinations were open to large error. Again, her conclusion is rather sweeping for the data at hand. Biology can gain nothing from such guessing on the basis of questionable data.—WILLIAM CROCKER.

Embryo of Welwitschia.—PEARSON¹⁸ has added to his former studies of *Welwitschia* a brief account of the development of the embryo proper. The small group of embryo initials at the tip of the suspensor first develops into a "massive meristematic group" of cells, in which the growing points of the embryo are organized, much as in *Ginkgo*, even the "lateral cones" being visible as small protuberances in the axils of the cotyledons. The suspensor increases in thickness greatly by centrifugal additions from superficial cells of the root cap, as in *Ephedra*. The whole intraseminal development of the embryo seems to be completed before the seed falls, and covers a period of about four months from the time of fertilization. A few seeds collected in 1907 germinated in 1910.—J. M. C.

¹⁷ ROSENBERG, ANNA, Ueber die Rolle der Katalase in den Pflanzen. Ber. Deutsch. Bot. Gesell. 28:280-288. 1910.

¹⁸ PEARSON, H. H. W., On the embryo of *Welwitschia*. Annals of Botany 24:759-766. pl. 64. 1910.

Morphology of Parthenium.—*P. argentatum* has become notable as the "guayule," or desert rubber plant, which is being exploited extensively in Mexico. In connection with its investigation for economic purposes, KIRKWOOD¹⁹ has investigated its life history, and also that of *P. incanum* and *P. hysterothorus*. It appears that in the guayule about 17 per cent of the seeds contain embryos, the numerous failures not being due to failure in fertilization, "but apparently to the cutting off of the nutritive supply in the later stages of development." The structures of the embryo sac, the development of the embryos, and spermatogenesis all seem to conform to the situations usual among Compositae.—J. M. C.

Structure of alpine plants.—A very considerable amount of asymmetry has been found by BLOCH²⁰ in the underground stems of certain alpine plants, notably in the rootstocks of *Anemone baldensis* and *Bartsia alpina*, the latter having a woody cylinder eight times as thick on one side as on the other. Among other peculiarities of these plants, the rootstock of *Geum reptans* is shown to have a cambium layer in the pith, and the older roots of two species of *Campanula* to develop an abnormal amount of lacunar tissue. An explanation of these phenomena will be sought in experimental studies.—GEO. D. FULLER.

Cretaceous conifers of Japan.—JEFFREY²¹ has called attention to the striking resemblance of the cretaceous coniferous flora of Japan, as recently described by STOPES and FUJII, to that of the Atlantic seaboard of North America. The resemblance is perhaps closer than the authors suspected, for JEFFREY claims that their proposed new genus *Yezonia* is in reality his *Brachyphyllum*; and that their *Cryptomeriopsis* is the same as the long-known *Geinitzia*.—J. M. C.

Establishment of the giant cactus.—From measurements of plants of various ages and a careful study of areas near Tucson, Arizona, containing several hundred individuals, SHREVE²² concludes that the giant cactus (*Cereus giganteus*) is not maintaining itself. No sufficient reason for this decadence is yet known. The average expectancy of life for this cactus in the Arizona desert seems to be about 175 years.—GEO. D. FULLER.

¹⁹ KIRKWOOD, J. E., The life history of *Parthenium* (guayule). Amer. Rev. Trop. Agric. 1:193-205. pls. 11-13. 1910.

²⁰ BLOCH, MADAME E., Sur quelques anomalies de structure des plantes alpines. Rev. Gén. Bot. 22:281-290. 1910.

²¹ JEFFREY, EDWARD C., On the affinities of the genus *Yezonia*. Annals of Botany 24:767-773. pl. 65. 1910.

²² SHREVE, FORREST, The rate of establishment of the giant cactus. Plant World 13:235-246. 1910.



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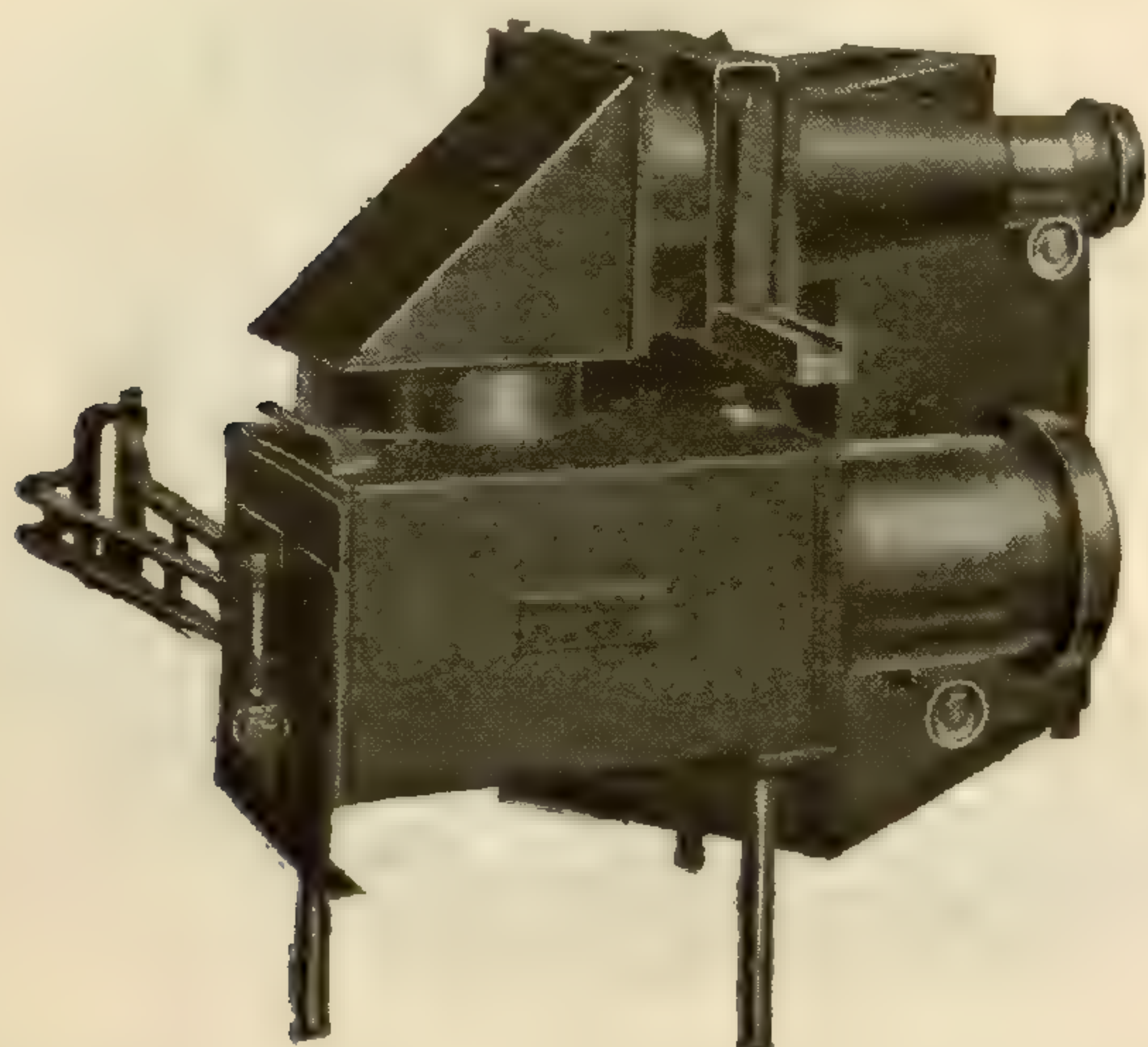
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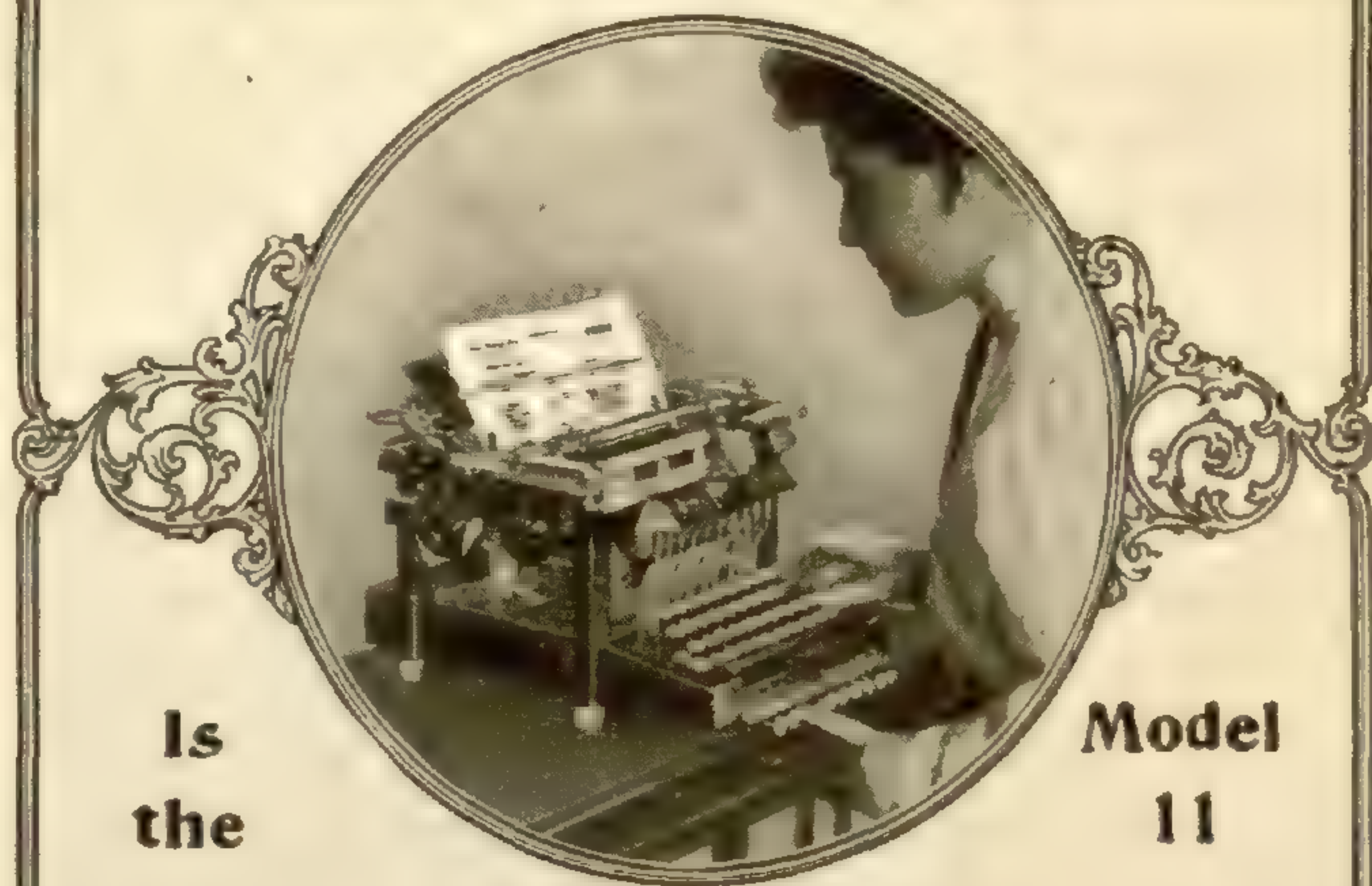
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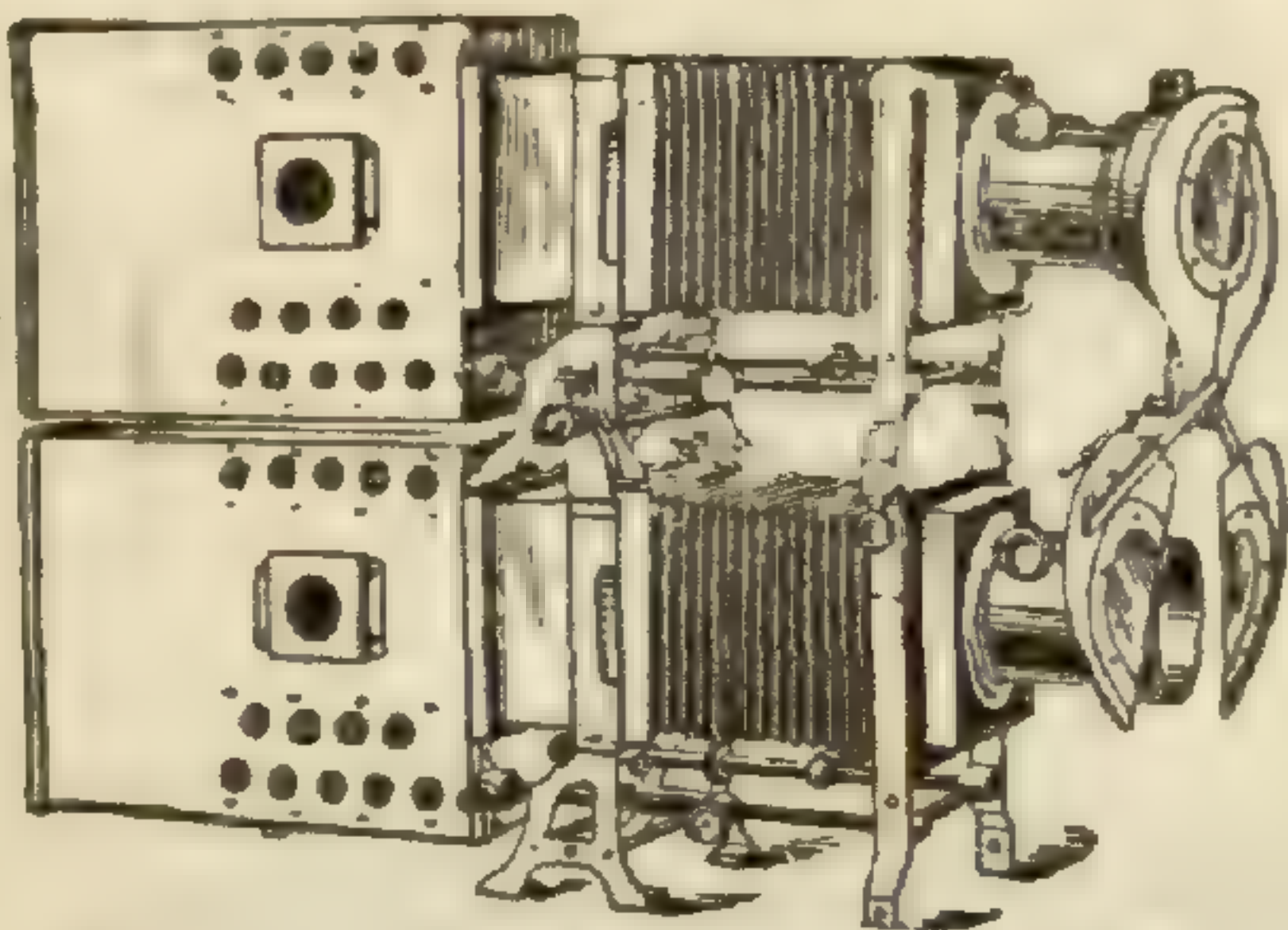
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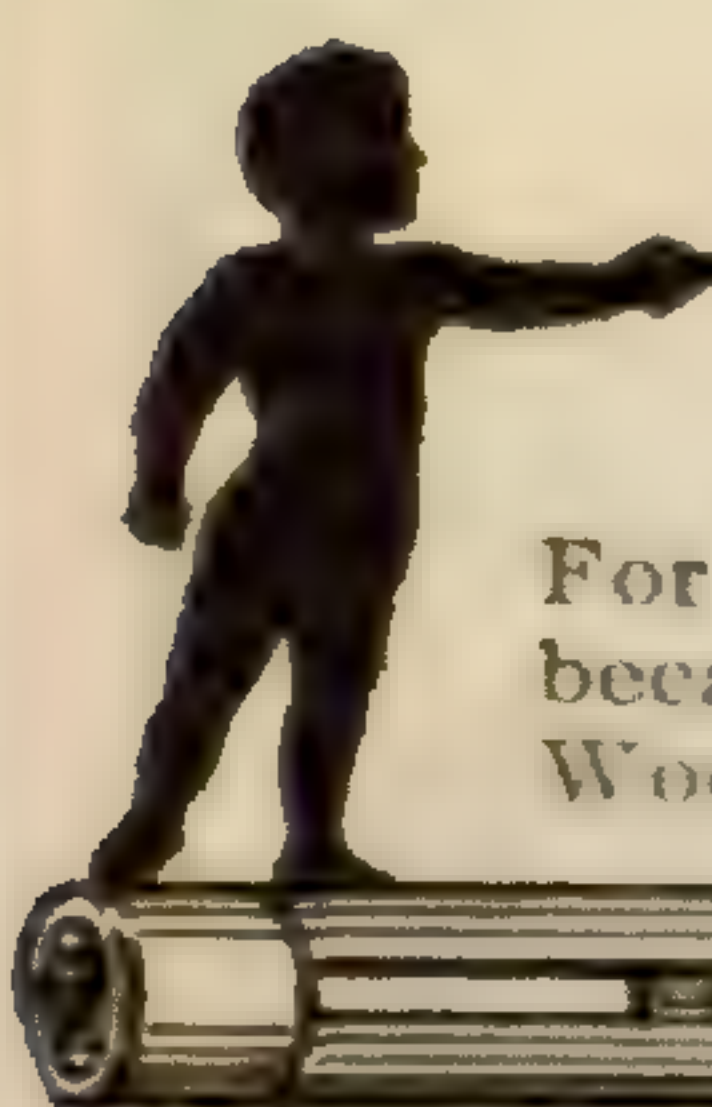
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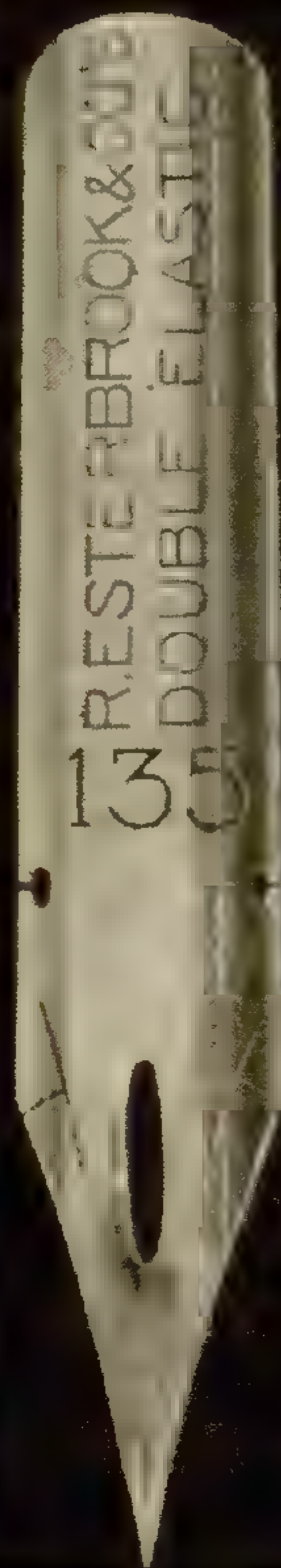
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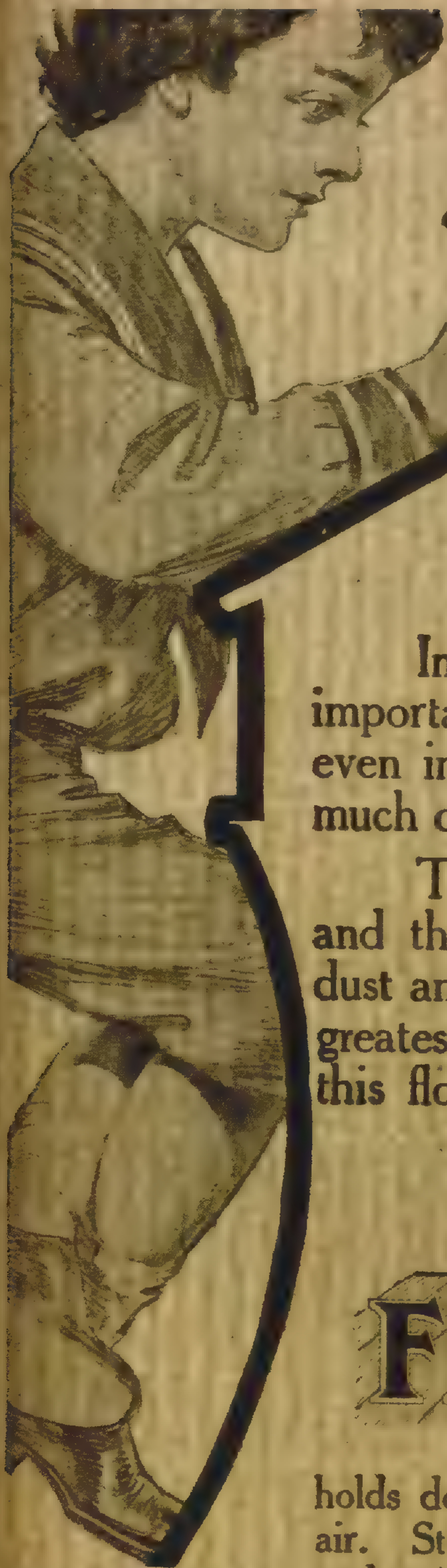
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THE
BOTANICAL GAZETTE

FEBRUARY 1911

THE ANATOMY OF THE SPORELING OF MARATTIA
ALATA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 142

GRACE MIRIAM CHARLES

(WITH PLATES IX-XII AND THREE FIGURES)

The Marattiaceae combine to a unique degree the interest of an extremely ancient family with the significance of connections not only with other fern families but with the origin of seed plants. The recent discovery of the latter connection calls for more knowledge of the vascular anatomy of the living Marattiaceae, based upon abundant material.

Historical

The first studies of the anatomy of the Marattiaceae were based upon the mature stem of *Angiopteris evecta*. As the anatomy of this genus is the most complicated in the family, the first investigators, DE VRIES and HARTING (7), in 1853, concluded that the vascular system is composed of a tangled net of bundles running in every direction through the stem; and that the strands make a spiral of several cycles, which finally run out into the leaf traces. They made no distinction between leaf traces, stem bundles, and cortical roots.

In 1864 METTENIUS (21) investigated the stem of a large plant of *Angiopteris evecta* that had been languishing for eleven years before it was used for research. He considered that the vascular tissue is arranged in a series of concentric meshed zones or funnels, whose apex is at the base of the main axis of the stem and whose obliquely running bundles pass off from the periphery as leaf traces; that these leaf traces contain a definite number of bundles from

the peripheral zone, with the addition of two strands from the second zone; and that the gap in the second zone is repaired by a strand from the third, and so on through the four or five concentric zones that compose the stele. Toward the top of the broad stem the strands united into broad bands. METTENIUS thought that this might be due to the unhealthy state of the stem he used. In 1900 Miss SHOVE (26), reinvestigating a mature stem of *A. evecta*, confirmed his theory. She found a further difference in her material in the absence of strands from the second zone in the leaf traces. Otherwise her results confirmed those of METTENIUS.

In 1877 DE BARY (6) accepted METTENIUS' description of the mature stem of *A. evecta*, but found in the young stem a typical fern cylinder. In 1889 KÜHN (17) extended the work on juvenile forms to *Kaulfussia aeschylifolia* and *Marattia fraxinea*. Their steles consisted of a cylinder of bundles surrounding a central strand, which fused with the peripheral cylinder and went out as part of a leaf trace. He supposed that the place of the central strand was taken by a peripheral bundle bending in to the center. In the older plants of *Marattia*, instead of one there were two concentric series of bundles in whose center again was a medullary strand. In *Kaulfussia* the central strand was single, in *Marattia* it was made up of different strands at different levels.

Two important contributions to the knowledge of the anatomy of the Marattiaceae were made in 1902. (1) FARMER and HILL (9) investigated the young sporeling of *A. evecta*, filling in gaps in their material with *Marattia fraxinea* and *Kaulfussia aeschylifolia*. They found in the sporeling a single solid protostele which passed by a medullated stage to dictyostely or solenostely as the gaps are repaired. They found that the skeleton of *Marattia* is simpler than that of *Angiopteris*, because the leaves are not so crowded, although the leaf gaps are larger. (2) BREBNER (3) found that the sporeling of *Danaea alata* also starts with a protostele which does not pass through a medullated stage, but becomes crescentic after the departure of a variable number of leaf traces, and passes directly into the solenostelic stage. The medullary strand arises as a branch from the interior of the solenostele.

JEFFREY (15) in 1903 examined young stems of several species

of *Danaea* and one specimen of *Marattia fraxinea*, all of which had reached the stage of an amphiphloic siphonostele with a medullary strand. He found a tendency of internal phloeoterma to degenerate, and lists the Marattiaceae with pteridophytes that have developed endarch collateral bundles. He gives no description or figures of the stele in this stage.

It is evident that there is a fundamental difference in the transition from protostele to solenostele in *Angiopteris* and *Danaea*, that there are other important points in the various accounts that do not harmonize, and that *Marattia* has been examined only incidentally from a few specimens. It seemed desirable, therefore, to make a thorough study of a large number of sporelings of *Marattia* in all stages of development.

Material

A very generous supply of sporelings of *Marattia alata* of various ages was sent from Xalapa, Mexico, in November 1908 by Professor BARNES and Dr. LAND, who described to me the places in which the young sporelings were found. The most favorable locations were on the east slopes of the mountains near Xalapa, at an altitude of about 1140 meters, the temperature averaging about 30° C. The rainfall is 250 cm. per year, and although it is not evenly distributed, the moisture supply is sufficient to support a dense tropical rainy forest. In some places the upper vegetation had to be cut away to allow enough light to reach the ground to see the sporelings and prothallia. The most abundant supply of sporelings grew on the steep bank of a mountain torrent, in a soil composed of volcanic ash and yellow clay. Many of the youngest plants grew under the shelves made by the washing down of the surface; in one spot they grew just out of reach of the spray from a waterfall.

The prothallium may persist until the sporeling has five or six leaves, or the sporeling may become independent when its primary root is only a few millimeters long. The smallest sporeling, illustrated in fig. 4, had a primary root about 4 mm. long, and a cotyledon of the same length, whose blade was just forked. As the leaf grows older, the veins dichotomize further, and the cotyledon becomes spatulate. The first four or five leaves are of this type,

then unequal dichotomy of the middle vein sets in. Soon two lateral veinlets become prominent and form the midribs of two lateral lobes. This begins at about the 25th leaf. More pinnae are added in the same way until the pinnate adult leaf is established. The primary root is sparsely covered with coarse root hairs to within a millimeter of the tip. Hairs are less numerous on the secondary roots; and in the later roots the endophytic fungus also is less than in the primary root. The cortex of the stem, growing downward around the primary root, carries the first leaf traces down. Decay early attacks the primary root and works upward into the base of the stem. The secondary roots grow to a great length in proportion to the size of the plant, and seldom branch. In specimens 4 cm. long and 1 cm. in diameter roots extend a meter or more from the plant.

The sporelings examined ranged from the small one described to plants 2-5 cm. in diameter and 5 cm. long. Fig. 5 shows the tuberous form, the persistent swollen leaf bases (*l*) which with the stipules (*s*) hide the surface of the stem, the roots (*r*) that penetrate the old leaf bases, and the apex (*a*) inclosed by the interlocking stipules of the young leaves. The tendency to dorsiventrality shown by older *Angiopteris* stems does not appear in *Marattia*; the slight bend in a few specimens might easily be due to conditions of growth. The upper half of three of the larger plants elongated in proportion to the diameter, giving a flask-shaped contour to the plants. On the neck of the flask the leaves were separated by 0.5 cm. This change of habit from the bulky leaf-covered base was accompanied by an important simplification of the vascular anatomy that will be described later.

Methods

Part of the plants were killed when they were gathered, in a mixture of 50 per cent alcohol and 4 per cent formalin; part were sent to Chicago in damp moss and killed in the laboratory in chromacetic acid. They were imbedded in paraffin and the small sporelings cut 10 μ thick, the large ones 15-20 μ . A week or more in the oven at 52° was necessary to infiltrate the older stems. The stain best adapted for general differentiation of

vascular tissues was found to be the safranin-anilin blue combination. Early stages in the development of mucilage ducts came out better in Delafield's hematoxylon and safranin.

A clear conception of the course of the bundles can be gained rapidly by building up a clay model molded to match section by section. Though the proportions are not exact in this free-hand method, the relation of the bundles to each other is as accurate as in the wax models, and the saving of time is enormous.

Investigation

In the development of the stele of *Marattia alata* three stages stand out sharply: (1) the protostele; (2) the amphiphloic siphonostele, or solenostele; and (3) the polycyclic dictyostele. The transitions from one stage to the next, because they are rapid and varying, are the points about which wide differences of opinion center. Of the two transitions, that from the protostele to the solenostele is the most variable among ferns.

PROTOSTELE TO SOLENOSTELE

In the Schizeaceae (BOODLE 1), the Cyatheaceae, and the Polypodiaceae (GWYNNE-VAUGHAN 11), the first appearance of parenchyma in the protostele is at the periphery of the protostele at points just above the departure of leaf traces. The transformation works gradually inward. The internal parenchyma is therefore always in contact with the cortical parenchyma. In the *Lindsaya* type of stem and in *Matonia* (TANSLEY and LULHAM 27, 28) internal phloem is differentiated within the xylem and comes in contact with the peripheral phloem at the leaf gaps. In *Pteris* (LECLERC DU SABLON 19) a pith develops within the xylem.

In *Helminthostachys* (LANG 18) the xylem, though sometimes solid, usually has parenchyma often conspicuous in the center, constituting a pith. Just below the origin of the first leaf trace the pith, if present, increases in size and is continuous with the parenchyma between the xylem of the leaf trace and that of the stele. If the stele is solid in the lower part of the internode, parenchyma appears in the center of the xylem in preparation for the departure of the leaf trace.

In *Angiopteris* (FARMER and HILL 9) certain cell rows in the solid protostele cease to differentiate as tracheids, and form a pith which rapidly increases in importance, for the leaf traces soon involve the whole thickness of the xylem ring. As soon as gaps are left, the annular appearance is lost, peripheral phloem dips down and borders the pith, and then internal endodermis is differentiated as a late and secondary occurrence. In *Danaea* (BREBNER 3) what appears to be pith separates the xylem of the outgoing leaf traces from the stele, and the stem passes at once from the protostelic to the dictyostelic condition.

In *Marattia* the protostele, usually solid at the cotyledonary node, may contain parenchyma cells, as in fig. 6. This is not definitely related to the center of the stele. When the first leaf trace goes off, a bay of the peripheral parenchyma may extend across the xylem. In this bay there may be isolated xylem elements which disappear later or join one or the other of the main xylem masses. The stele may become solid above and repeat the same process in giving off 4-9 more leaf traces, or it may contain scattered parenchyma from this time on. In the latter case the line of division for the next leaf trace is marked by the largest area of inclosed parenchyma. As in *Danaea*, a combination like the simultaneous departure of two or more leaves, or of a root and leaf, may give a temporary annular appearance (fig. 7), where the root trace (*rt*) is going off opposite the leaf trace (*lt*).

The stele may return to the solid protostele above such a cylindrical stage. The first leaf traces may take off half of the elements of the protostele. Later, the stele increases in size in proportion to the leaf traces, so that the line of division between stele and leaf trace cuts in a curve instead of straight across the stele (text fig. 1). Phloem and endodermis close in behind the leaf trace over the concave as over the plane surface of the protostele (fig. 8). Soon a leaf trace goes off from the side opposite the curve before it has rounded out (fig. 9). This leaves two segments of the stele separated by parenchyma (fig. 10). The diagrams (figs. 11-21) show the start of the next leaf trace, the penetration of phloem into the stele from the opposite side (figs. 13-15), its withdrawal as the strands close together (fig. 16);

also the repetition of this process for the next leaf, when the phloem closes around the xylem strands (fig. 17) and then disappears on the side where the former leaf went off (fig. 18). At the departure of leaf 3, endodermis as well as phloem penetrates between the two xylem strands (fig. 19), and in fig. 20 the cylinder with internal phloem and endodermis is established. The transition from protostele to solenostele with leaf gaps is represented in text fig. 1.

Angiopteris, *Danaea*, and *Marattia* agree more closely in structure than in interpretation of the tissues concerned in this transition from protostele to solenostele. The difference in interpretation involves the question whether the tissue not xylem within the endoderm is cortical or stelar. FARMER and HILL (9) are inclined to regard only vascular tissues as stelar. This leads to the difficulty of determining what tissues are vascular and what are cortical when there is no histological differentiation. At one level they regard a tissue as xylem parenchyma which in another closely related section they call pith (9, pl. 16, figs. 10, 11). The confusion caused by setting aside as non-vascular the pith in the Marattiaceae is the greater because of the widespread tendency to lignify only part of the xylem parenchyma. The primary as well as later roots may have a solid xylem core, or may be lignified only at the poles. The cotyledonary node, usually solid, may contain scattered parenchyma, and the bundles of the dictyostele have extensive bands of parenchyma (fig. 22). Another difficulty in the way of regarding this pith as non-vascular in the Marattiaceae is that the parenchyma is rarely definitely localized in the center of the stele, so that similar stages in the development of the stele of two plants of the same species would demand as different interpretations as those given to *Angiopteris* and *Danaea*. On the other hand, the parenchyma



FIG. 1.—Diagram model of young stem in transition from protostele at the base to siphonostele at the top; the leaf traces leave constantly deeper crescents in the stele.

that appears to separate the xylem of the outgoing leaf trace from the stele cannot be lightly dismissed, for the early appearance of this tissue related to more than one leaf is probably the origin of the pith in the Marattiaceae.

The obscurity of this transition is due to the telescoping of the dictyostelic into the protostelic stage. A slight extension of this process would result in the simultaneous origin of two or three leaves at the cotyledonary node, from which a dicotyledonous habit may have been derived in some offshoot of the family.

Rarely the solenostele forms a complete cylinder. It is generally broken by two or more leaf gaps, whose large size and close arrangement cause them to overlap. At this stage the bundle arrangement is like that in the Dicksonieae, some of the Polypodiaceae, and *Ophioglossum*. The last differs from the others in the collateral structure of the bundles. In some stems of *Marattia* the tendency toward a reduction of internal phloem and endodermis, referred to by JEFFREY (15), appears. This is not uniform, however, and is more likely to appear in the medium sized than in the larger stems.

THE MEDULLARY SYSTEM

When the stele reaches a diameter of 2-4 mm., a medullary strand appears and initiates the final stage in the development of the stele. It may originate in three different ways: (1) Most commonly it branches from the inner surface of the solenostele. Protophloem, otherwise absent on the inner surface of the stele, appears in a patch, which is bulged outward by an increase in parenchyma (fig. 23, *pph*), and later xylem elements increase at that point. Usually a root is given off from the external surface of the bundle opposite this branch (fig. 24). This is the origin described by FARMER and HILL (9) and BREBNER (3) as a "local hypertrophy of the internal phloem." (2) It may arise by a branch which runs into the pith from the upper part of the margin of a leaf gap. (3) The pith may develop a cambium which gives rise to a strand of phloem in the center of which xylem then forms. The xylem may run 0.3 mm. before a commissure connects it with the main vascular system.

The course of the medullary system is relatively uniform in different stems. The strand runs upward through the medulla toward a leaf gap that is about to close (fig. 25). It joins one of the margins of the gap, the strand on the other margin closes in, and the three strands form a plate of vascular tissue from whose outer surface a root usually goes off (fig. 25, *rt*). The medullary strand soon frees itself again while a leaf trace goes off from the vascular plate above the point where the medullary strand joined the main vascular system. Farther on in its course the medullary strand sends a short branch into the main system, and this is not given off again but goes out with a leaf trace (fig. 25, *ms*). As the leaf traces become more crowded (text fig. 2a) the medullary strand divides into a greater number of parts, which join the main system at the closing of the leaf gaps. Occasionally a gap closes without a strand from the medullary system. At this stage *Kaulfussia* (17) and *Archangiopteris* (12) closely resemble *Marattia*.



FIG. 2a.—Exterior view of diagram model of the stele at the stage when the medullary strand appears; the medullary strands can be seen through the upper leaf gap.

Further complications of the medullary system of *Marattia* come from combinations of anastomoses and branching (text fig. 3). In *Matonia* the second cylinder is developed from the solid central strand

in the same way that the protosteles in it become siphonosteles, by the differentiation of a strand of phloem in the center of the xylem. This repetition of the process by which the first cylinder was made does not take place in *Marattia*, but the medullary sys-

tem becomes cylindrical by the anastomosis of two central strands (text fig. 3) in one case, although there are suggestions that the cylinder may also be formed by the branching of the strand as KÜHN (15) suggests. In the one clear case of the formation of the second cylinder in my material two medullary strands fuse to form a crescent. A branch from one horn of the crescent passes over to the other horn, then a strand from the first horn is cut off and runs out to a leaf gap. Further branching breaks up the secondary solenostele.

On account of the spiral arrangement of

the leaves, the medullary strand that shares in closing a leaf gap at one level makes part of the vascular tissue of the leaf above in that rank. When the crowding of the leaves breaks the regularity of the spiral the medullary strand is less definitely related to the leaf traces. The influence of the compact form of the stem is further emphasized in the stems described above whose upper half elongates. In these the medullary strand



FIG. 2b.—The same as fig. 2a, with the side cut away to show the course of the medullary strand.

branches less and less frequently, until it finally joins the main vascular system and is not given off again (fig. 25). At the same time the strands of the main vascular system unite into a solenostele with a single leaf gap. This is the same sort of behavior as that in the plant examined by METTENIUS (21). The compact habit of *Marattia* is therefore responsible for two of its most striking differences from the *Psaroniae* (22): the shape of the bundles, which are band-shaped in *Psaronius* and elliptical in *Marattia*; and the relation of the medullary system to the leaf traces.

The relation of the roots to the external and to the medullary systems differs in the mature stem examined by Miss SHOVE (26) and in the young stems of *Marattia*. In the latter the main root supply joins the external system, while the medullary system has a few small roots. In *Angiopteris* the largest number of roots is attached to the internal system. This difference may be due to the greater importance

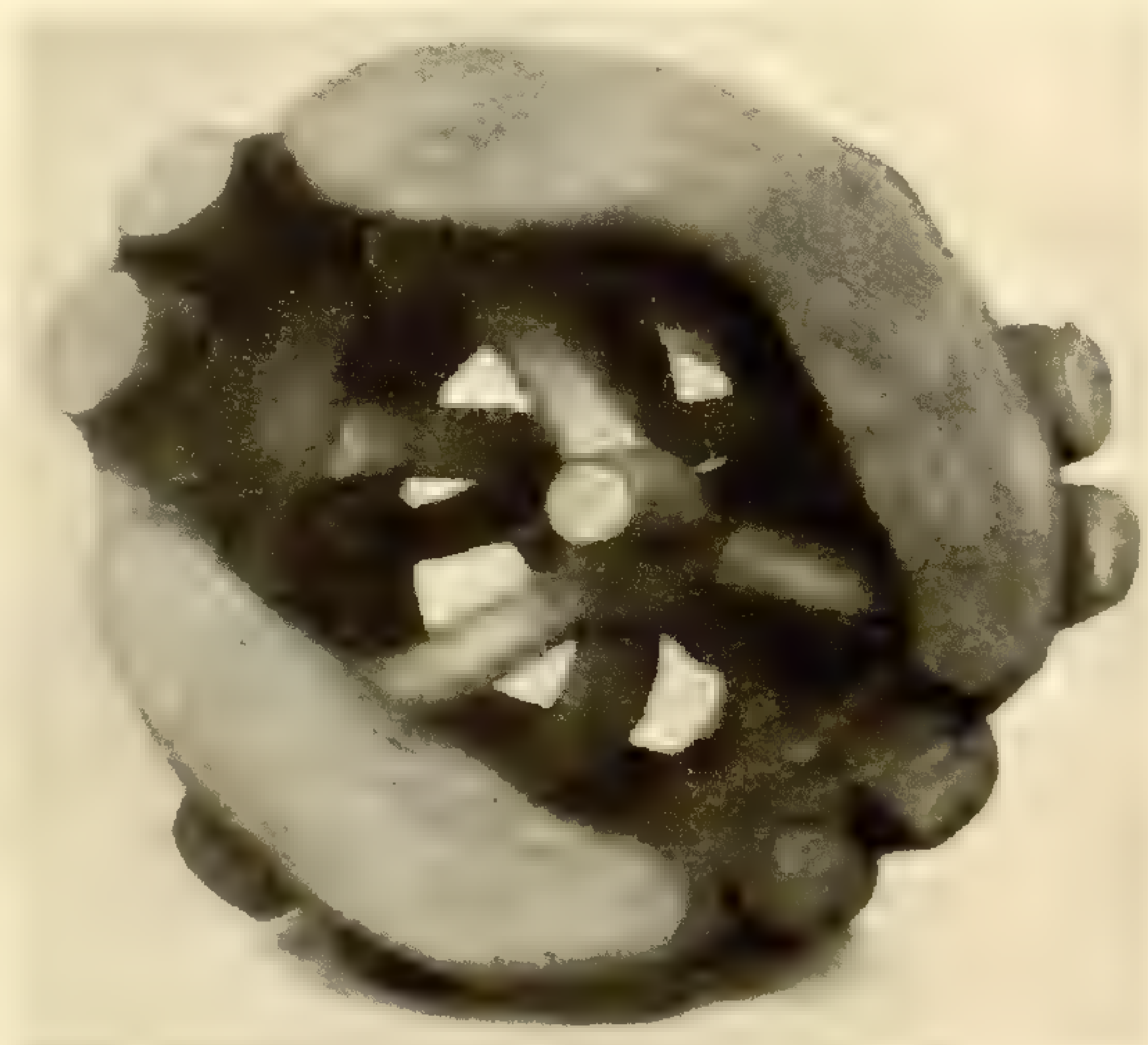


FIG. 2c.—Upper end view of fig. 2a.

of the internal system in the older stem, or to the possibility that the meshes that apparently belong to the external system in the mature stem really belong to the leaf traces, and the second zone is homologous with the main vascular system to the young stem.

In comparing the medullary systems of *Marattia* and the solenostelic ferns described by GWYNNE-VAUGHAN, some important differences appear. In the latter the origin of the system is the elaboration of a thickened leaf gap margin. The thickening works upward and downward, and in *Alsophila* (11) the strands are decurrent into the pith. In *Marattia alata* the origin is from an internal branch above a leaf gap, from the top of a leaf gap, or from a cambium in the medulla. In the solenostelic ferns the connections of the medullary with the main vascular system are generally at the nodes and along the leaf gap margin, although in *Pteris elata*

it connects at the anterior end of the leaf gap. In *M. alata* it joins the external system in the internodes, is freest at the nodes, and is concerned with the closing of the leaf gap. In the solenostelic ferns roots are not connected with the internal system as they are in the Marattiaceae. In such solenostelic ferns as have more than one concentric cylinder in the medullary system, as in *Matonia*, the



FIG. 3.—View from the upper side of a model, showing the origin of a medullary cylinder from the anastomosis and branching of two medullary strands.

formation of the second cylinder is markedly different from that in *Marattia*. In the Cyatheaceae the medullary strand takes part in the formation of several leaf traces, in *Matonia* it is a definite part of a single trace. In *Marattia* it shares in forming the region from which a leaf trace goes off.

If the medullary system of Marattiaceae is homologous with that of the Dicksonieae, Cyatheaceae, and Polypodiaceae, modifications must have taken place in the Marattiaceae. The place of

origin must have shifted upward and sidewise, so as to come above a leaf trace instead of along the margin of the gap left by it, as has taken place in *Alsophila*. The later connections must have made the same change in relative position of internal and external systems. In view of the wide distribution of medullary strands in remote groups of the pteridophytes, however, it is not certain that they are homologous even in these closely related families.

A comparison of the young stem of *Marattia* with that of *Psaronius* shows some points of resemblance more sharply than appear in the mature vascular system. The band-shaped bundles, the close relation of the medullary system to the leaf traces, and the simple leaf traces are alike in the young *Marattia* stem and in *Psaronius*. The absence of roots on the medullary system of *Psaronius* may be due to the relatively small gaps in the peripheral cylinder. The slight relation of the peripheral bundles to the leaf traces may be due, as RUDOLPH (21) has suggested, to the ranked or simple spiral arrangement of the leaves. It may be that the tendency to free origin and ending of medullary strands in *Marattia* indicates a reduction from the high state of development of such strands in *Psaronius*, as such similar free endings have been interpreted in the petioles of *Ceratozamia* (DORETY 8) and *Botrychium* (CHRYSLER 5).

PROTOXYLEM

The variability of protoxylem noted by GWYNNE-VAUGHAN (11) and TANSLEY (28) in Filicales generally reaches a high expression in *Marattia alata*. The first xylem elements to develop appear at the cotyledonary node. They may be the slender spiral tracheids common in ferns, similar small vessels with reticulate thickenings, as in *Dicksonia apiifolia*, or stretched scalariform vessels of the same caliber as the other elements of the xylem strand; or there may be no distinction between the first vessels and those developing later as in *Angiopteris* (FARMER and HILL 9) and *Danaea* (BREBNER 3). In the last case the change to the primary root is brought about by a reduction in the xylem at opposite sides of the bundle, development of protoxylem at the ends of the xylem band, and disappearance of phloem at the ends and increase at the sides of the xylem. In two primary roots there were three poles instead

of the two that prevail generally. As the pericycle is delicate and irregular, the protoxylem of the root often abuts on the endodermis.

In a few specimens spiral exarch protoxylem is present in the cotyledonary node. This is continuous with the protoxylem at the poles of the primary root and in the first leaf trace. In other stems the mesarch position characteristic of the older stem appears at the cotyledonary node. The same unsettled condition persists in the solenostele, although an examination of the apical region shows that the first elements lignified are toward the center of the stem. In the strands of the dictyostele definite protoxylem points appear in an endarch position, with occasionally one or two centripetal elements beyond them (fig. 22). These bundles do not show the distinction between large bundles with mesarch or no protoxylem, and small strands with endarch protoxylem observed in *Angiopteris*.

The cotyledonary trace shows the same kind of variations in the position of the protoxylem as the cotyledonary node. It may be exarch where it joins the stele (fig. 26) and gradually shift to mesarch (figs. 26-30) in the petiole; no protoxylem may be distinguishable in the trace near the stele, but a development of it in a mesarch position occurs while the trace is passing through the cortex; or the trace may consist of only two or three scattered elements. The next three or four leaves are mesarch, and may become endarch in the upper part of their course. The older leaf traces are endarch as in *Angiopteris* and *Danaea*.

APICAL MERISTEMS

The apical regions of *Marattia* have been the source of much difference of opinion. HOFMEISTER (13) described a single deep triangular apical cell for the Marattiaceae, as for all other vascular cryptogams. According to HOLLE (14) a four-sided apical cell is found in the stem of the young sporophyte and is retained permanently. BOWER (2) describes for mature plants a 4 or 5-celled meristem meeting at the intersection of two more or less perpendicular lines. CAMPBELL (4) found that in some cases at least the apex of the stem is occupied by a single initial. FARMER and HILL (9) describe an apical cell of irregular prismatic form,

though sometimes triangular in cross-section, in the apex of the young stem of *Angiopteris*, and BREBNER (3) concluded that *Danaea* was the same.

Such differences of opinion show that there is either variation or vagueness in the structure observed. In this case both enter into the result. In very young stems there is a triangular pyramidal apical cell (fig. 31). This soon becomes prismatic, and the outline of the triangle in cross-section becomes irregular (fig. 32). Gradually it becomes four-sided (fig. 33). Then one of the latest segments begins to act as an apical cell, and there are two blocks of meristematic cells at the apex (fig. 34). In longitudinal view two sections separated from each other show two large vacuolate cells cutting off segments from the base. The division of the segments is very irregular. In a still larger stem the apex was occupied by a meristem (fig. 35).

The growing point of the young stem is close to the base of the youngest leaf and very narrow (fig. 36). As the stem grows older the apex grows broader. At the solenostelic stage the tissue below the center of the apical cell is large-celled pith (fig. 37).

The root apex has received more attention than that of the stem. The three-sided cell, probably derived from the octant of the embryo, has been observed in *Angiopteris*. A similar cell occurs in the apex of the very young primary root of *Marattia*. As in the stem, a four-sided prism soon appears, which HOLLE (14) thought was permanent. SCHWENDENER (25) held that it divided into four about the axis of the root, and BOWER (2) agreed with him. RUSSOW (23) found a group of initials. KOCH'S (16) explanation for the different situations that occur is ingenious. The evidence, however, of a regular sequence of divisions and fan-shaped growth of one segment with consequent shifting to the center is not entirely convincing. A possible explanation is that there is no fixed structure or behavior in the apex of the root.

New roots originate in the meristematic region of the stem before differentiation of tissue has begun. FARMER and HILL (9) maintain that the origin is a single six-sided prismatic cell of the endodermis cutting on the sides and ends. According to DE BARY (6)

root origin in pteridophytes, with the exception of Lycopodiales, is endodermal, as contrasted with the prevailing pericyclic root origin in seed plants. In *Marattia* the pericycle is not a true pericycle, since it is composed of sister cells of the endodermis, and the phloem may abut on the endodermis. Roots originate within the undifferentiated cylinder (fig. 38). Periclinal divisions work outward and laterally (fig. 39) and into the cortex which forms the periblem of the young root (figs. 40, 41).

The chief work on apical regions was done under the influence of HANSTEIN'S theory of a rigid morphological distinction between periblem, plerome, and dermatogen. SCHOUTE (24) has shown that the apical divisions do not determine the limits of the tissues developed from them. This leads to the view that the character of the apical region is determined by the bulk of the organ and has no other significance. Whether the transition from the fernlike apical cell to a meristematic region has any phylogenetic significance, must be determined by finding whether other bulky plants show this variability. Some species of *Setaginella* have more than one apical cell (Rusow 23), but with this exception *Marattia* is unique in this character.

MUCILAGE DUCTS

Soon after the solenostelic stage is established, a mucilage duct may appear in the center of the pith. A branch from it runs out along the adaxial side of each leaf trace, and branches and anastomoses in the cortex of the stem and petiole. FARMER and HILL (9) follow KÜHN (19) in ascribing a lysigenous origin to these ducts. BREBNER (3) holds to the schizogenous origin in *Danaea* at the upper ends of the ducts. *Marattia* resembles *Danaea* in the division of the parenchyma cell into four to six without increase in size, and the separation of the walls where the small cells come together. The contents of the small cells stain deeply with anilin blue, and the nuclei, gathered around the point where the cells are to break apart, are small and denser than the nuclei in the surrounding parenchyma cells. The space left when the walls break apart appears empty at first, then becomes filled with a vacuolate substance that stains with anilin blue. Later the reaction of this

mucilage to stain changes rapidly and it takes the safranin. At this time and earlier than in *Danaea* the small cells begin to break down and the mucilage becomes stringy (fig. 41). The small cells do not break down uniformly; they may extend into the cavity of the duct as the "bridge-cells" of *Danaea* or float in the mucilage. The schizogenous stage may be omitted and cells of the pith break down into mucilage directly. Although tannin cells are numerous, none appeared to be changing to mucilage ducts as LUTZ (20) describes for *Angiopteris*. The origin and development of the mucilage ducts in the seedling of *Microcycas* are identical with those of *M. alata*.

Summary and conclusions

1. The transition from protostele to solenostele in *Marattia* is sudden and without the intervention of a definite medullated monostelic stage. The indefinite hints of pith due to the early start of parenchyma to divide leaf trace from stele may be the origin of the medullated stage.

2. The medullary system of *Marattia* differs from that of the solenostelic ferns in origin, course of bundles, and development into a cylinder. It resembles that of *Psaronius* in its relation to leaf traces.

3. Elongation of the stem causes the union of the bundles into broad bands and a reduction of the medullary system. This emphasizes the close relation between the compact habit and crowded leaves of *Marattia* and the number of concentric cycles and leaf gaps in the dictyostele. The difference in habit, therefore, accounts for the difference in the anatomy of *Marattia* and the more elongated Marattiaceae, *Danaea*, and *Kaulfussia*, and the treelike *Psaronius*.

4. The occurrence and position of protoxylem varies. It may not be distinguishable or may consist of spiral or modified reticulate tracheids. When distinguishable, it may be in an exarch or mesarch position in the cotyledonary node, mesarch in the protostele above the cotyledonary node, and usually endarch in the strands of the older parts of the stem. Similar variations occur in the leaf traces. The cotyledonary trace may change from

exarch to mesarch, the later leaves from mesarch to endarch. Mature leaf traces are endarch.

5. Apical meristems vary from the fernlike triangular apical cells in young sporelings to meristematic groups in older stems and roots. Such variation during the course of development occurs in the gametophytes of pteridophytes and in some liverworts, but is not recorded for the sporophyte of other ferns.

6. The cotyledonary trace is collateral during most of its course. Later leaf traces start collateral and develop adaxial sieve tubes in their course through the cortex. Some stems show a slight tendency toward a reduction of internal phloem and endodermis, others an increase in the older part of the stem. The basis for classifying the Marattiaceae with pteridophytes that have developed collateral bundles is therefore insecure.

7. Secondary roots originate from vascular tissue before differentiation into regions has begun. The cortex shares in forming the cortex of the root.

8. Mucilage ducts originate both schizogenously and lysigenously, generally the former.

Marked instability is characteristic of *Marattia*. The Ophioglossaceae share this trait in root structure, the Dicksonieae in protoxylem position. Only gametophytes have such a transition of apical regions. Combined with variability is the indefiniteness of the medullated monostelic stage. Such instability is characteristic of plants that give rise to new lines. It is evident that the Marattiaceae have retained many characters of the stock from which branched off the Ophioglossaceae, then the Psaronieae and Cyatheaceae. It is probable that the compact habit of the Marattiaceae was developed after the lines connecting with the other families had diverged, since the characteristics due to it are also unstable.

This investigation was carried on at the University of Chicago, under the direction of Professor JOHN M. COULTER and Dr. W. J. G. LAND, to whom I wish to express my thanks for criticism and advice.

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EXPLANATION OF PLATES IX-XII

With the exception of figs. 4, 5, 11-21, and 25, all drawings were made with the aid of an Abbé camera lucida and reduced one-half in reproduction. Abbreviations are as follows: *c*, cotyledon; *en*, endodermis; *l*, leaf; *lb*, leaf base; *lt*, leaf trace; *ms*, medullary strand; *pa*, parenchyma; *ph*, phloem; *pph*, protophloem; *pr*, prothallium; *px*, protoxylem; *r*, root; *rt*, root trace; *s*, sieve tube; *st*, stipule; *x*, xylem.

FIG. 4.—Young sporeling attached to the prothallium, with the second leaf appearing. $\times 2.5$.

FIG. 5.—Older sporeling, showing persistent leaf bases (*lb*). $\times 1$.

FIG. 6.—Transverse section through the cotyledonary node, showing parenchyma cells among the xylem. $\times 400$.

FIG. 7.—Transverse section through the stele, showing apparent pith due to the simultaneous departure of the root trace (*rt*) and leaf trace (*lt*) opposite each other. $\times 188$.

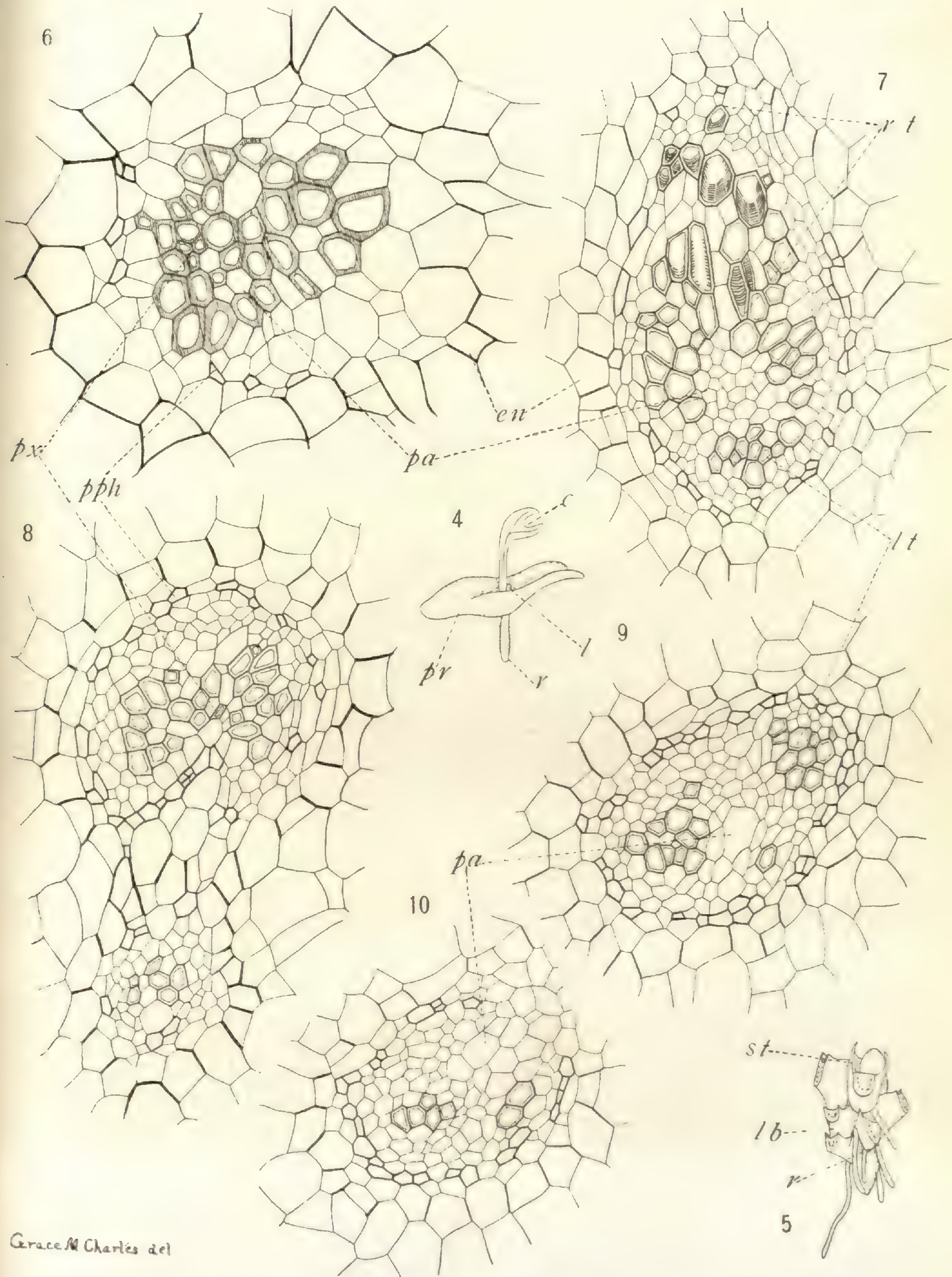
FIG. 8.—Transverse section of the same 50μ above fig. 7, showing phloem (*ph*) and endodermis (*en*) cutting in a curve behind a leaf trace. $\times 188$.

FIG. 9.—Transverse section of the same 40μ above fig. 8, showing the departure of the next leaf trace (*lt*) and a persistent cell of cortical parenchyma (*pa*). $\times 188$.

FIG. 10.—Transverse section of the same 40μ above fig. 9, showing cortical parenchyma (*pa*) at the side of the stele, contrasting with xylem parenchyma in size. $\times 188$.

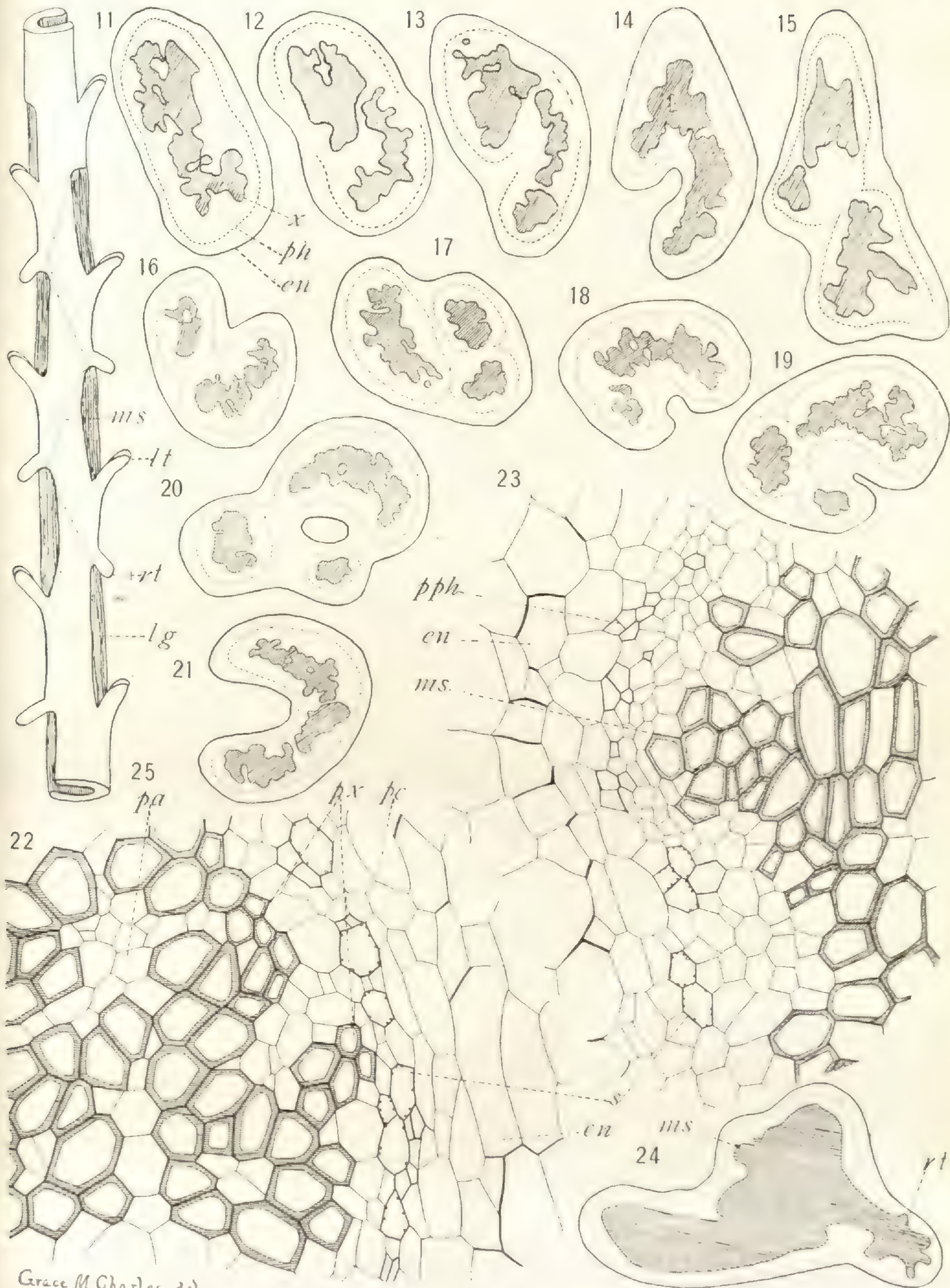
FIGS. 11-21.—Diagrams of successive stages in the transition from protostele to solenostele.

FIG. 22.—Transverse section from the inner surface of a dictyostelic bundle, showing endarch protoxylem, bands of parenchyma, sieve tubes, pericycle, and endodermis. $\times 188$.



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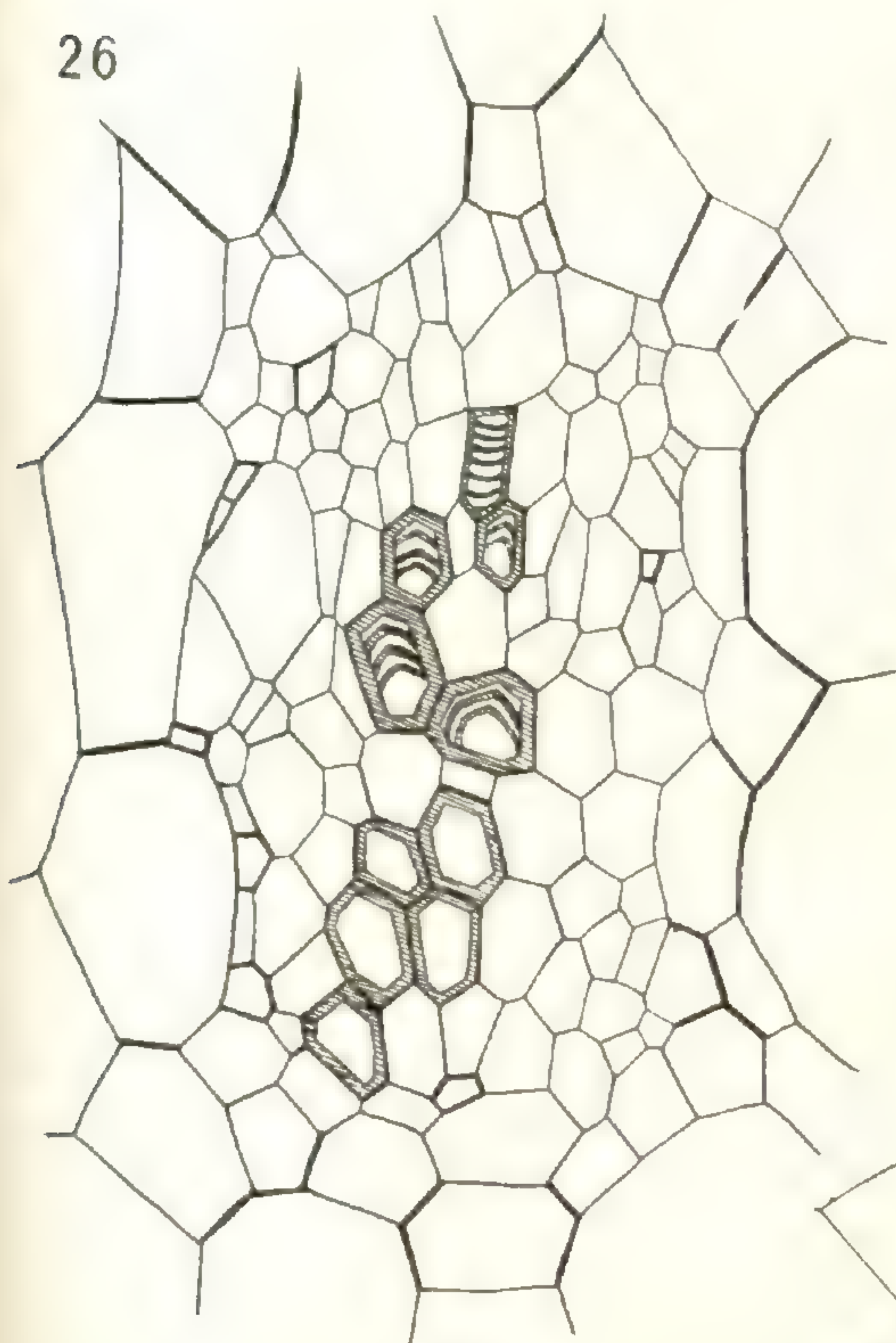
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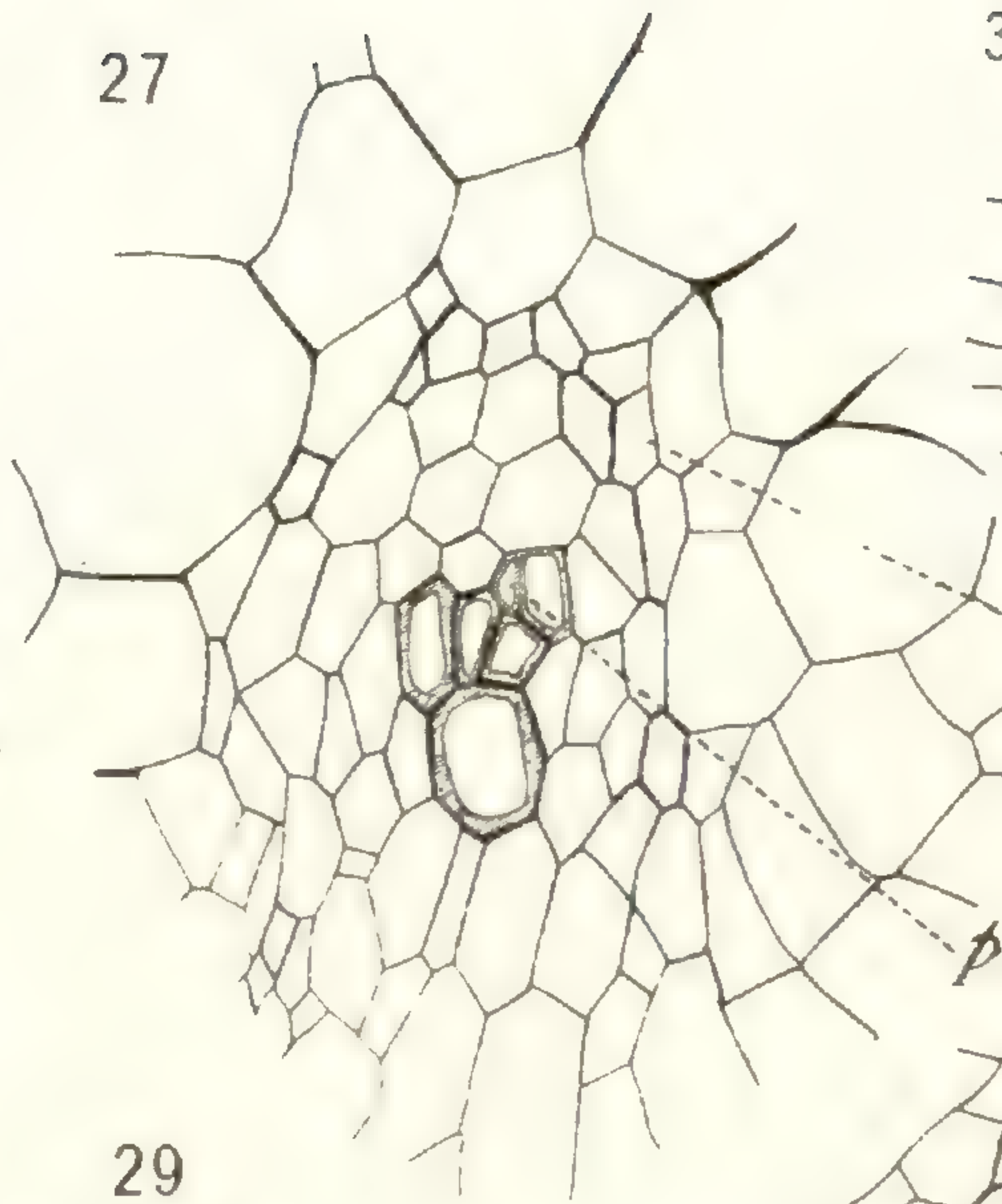
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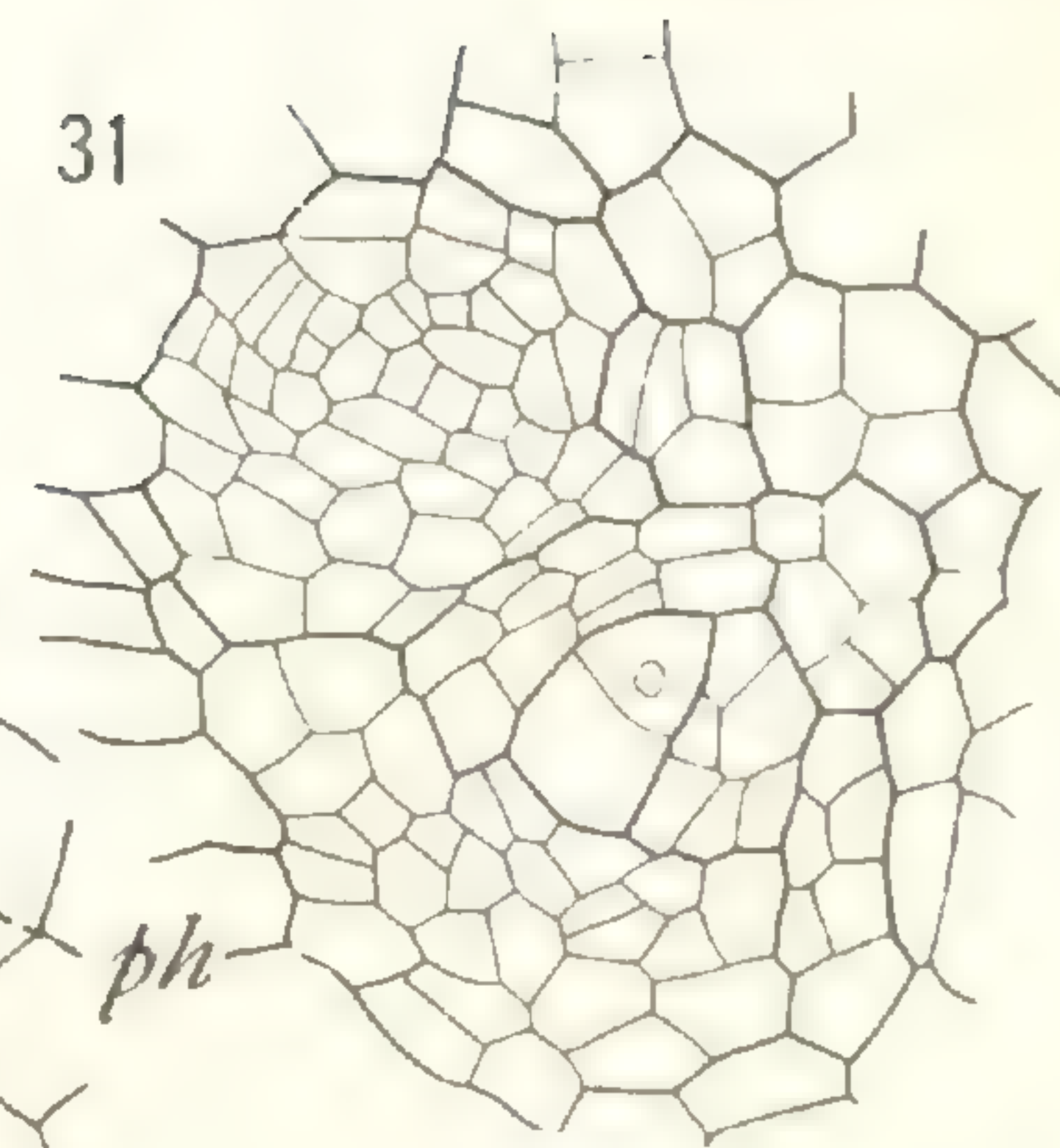
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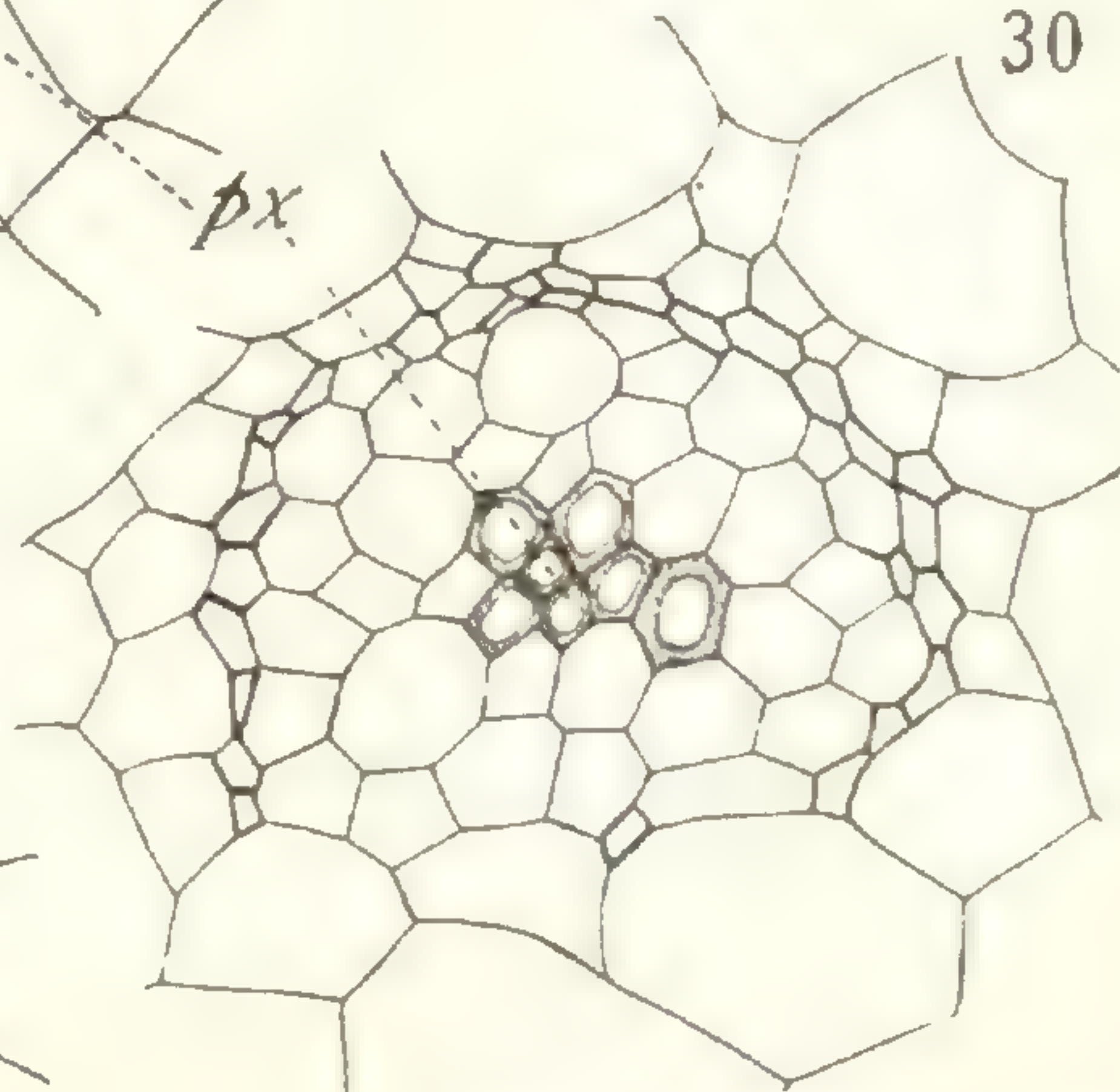
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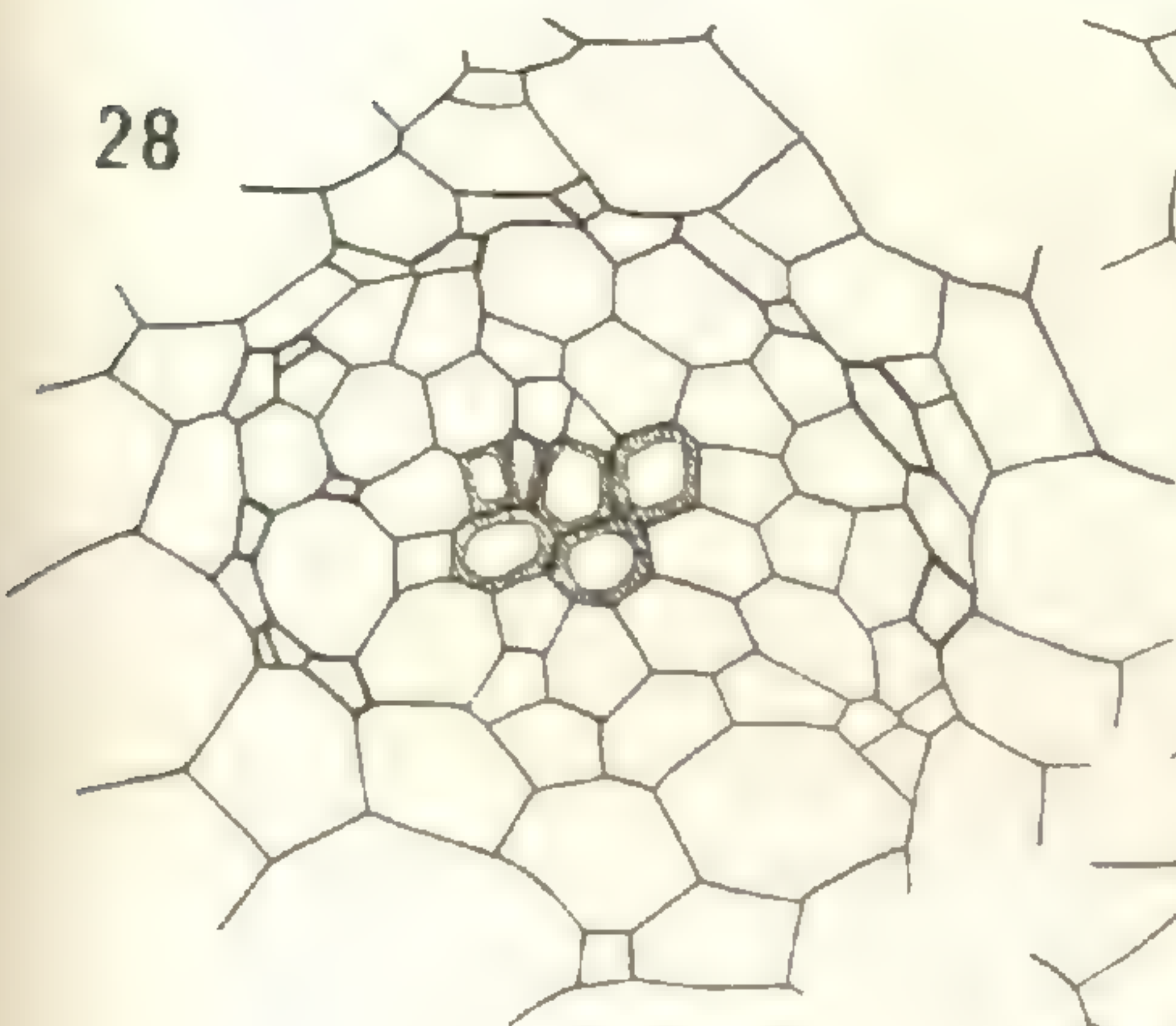
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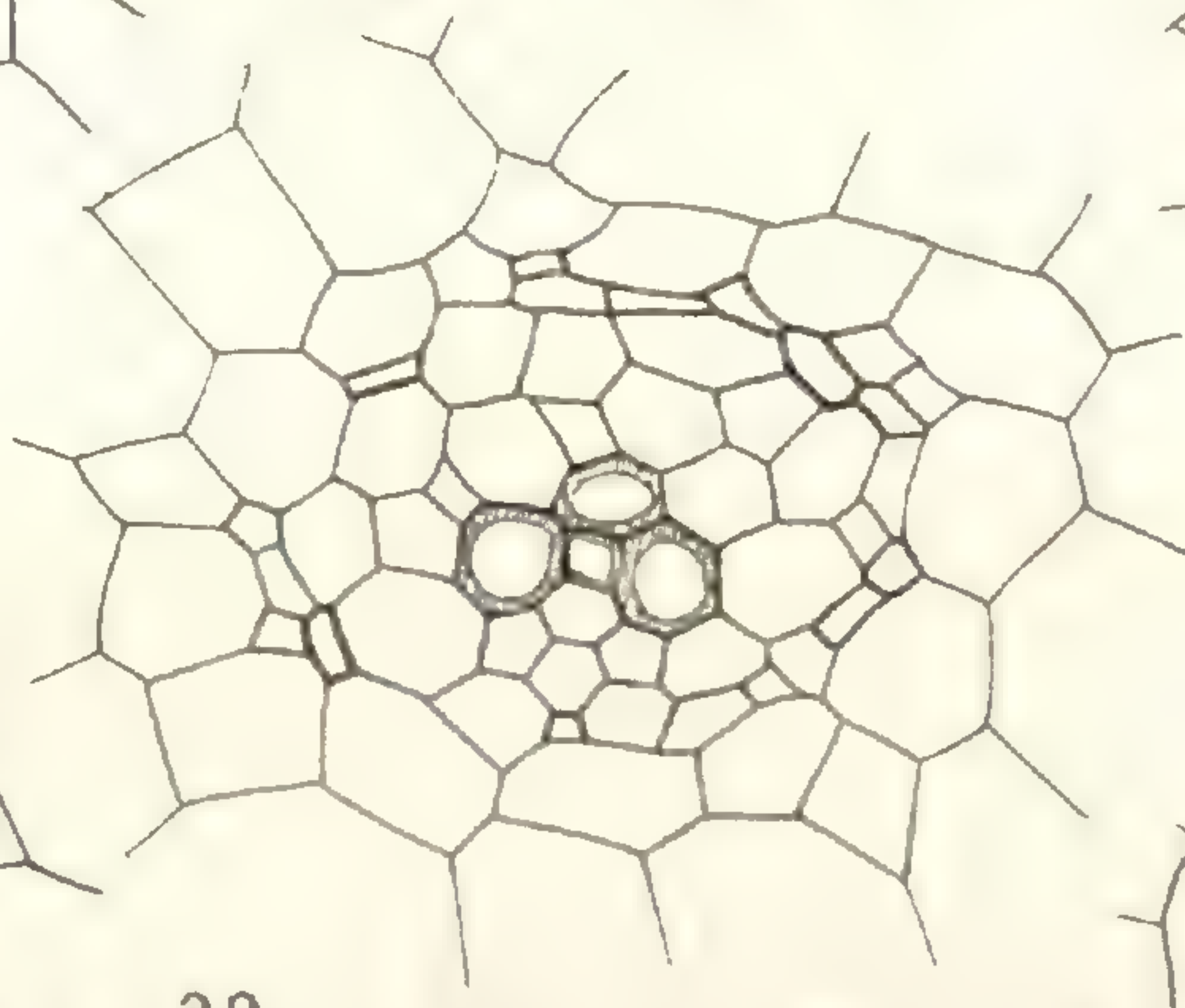
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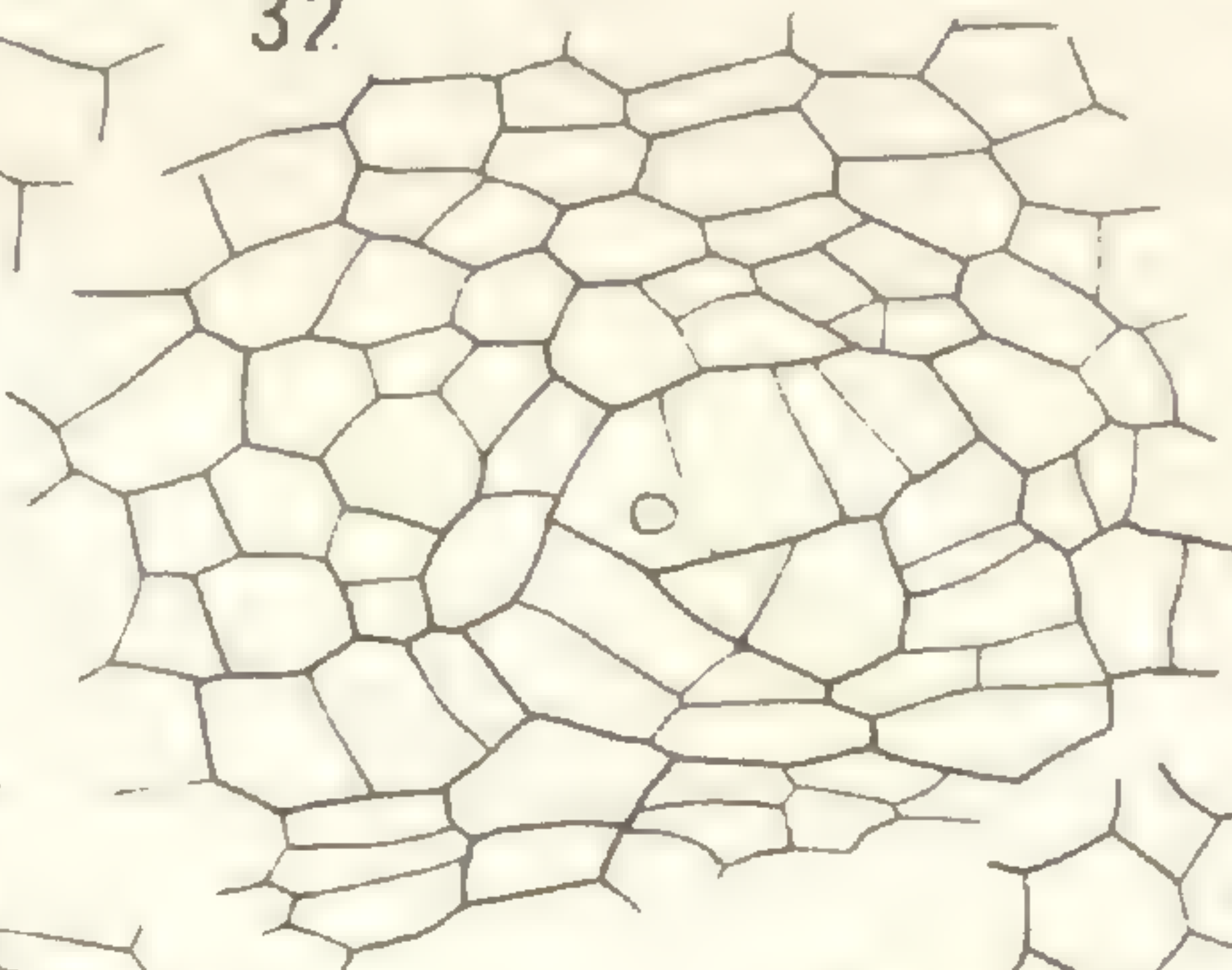
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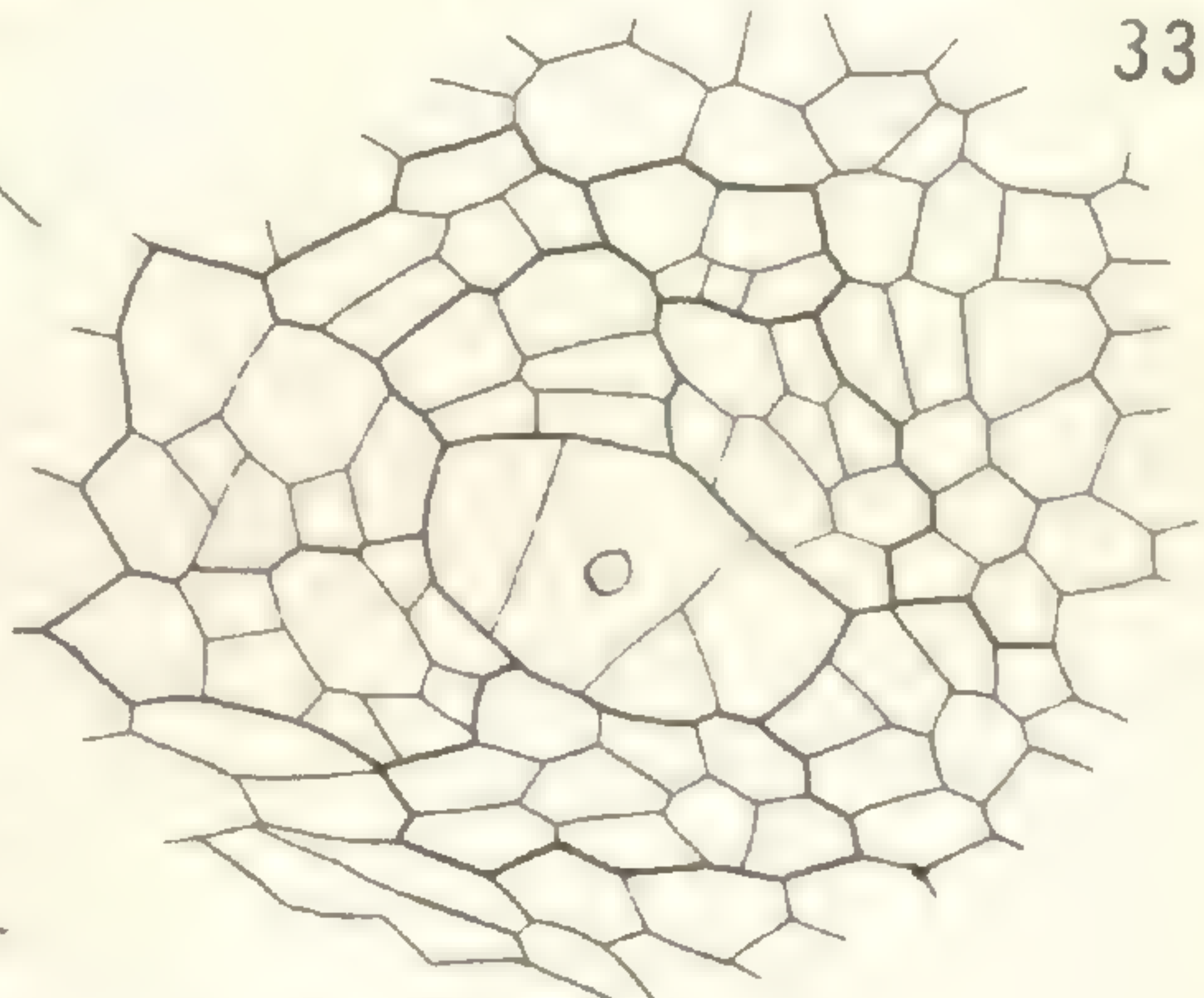
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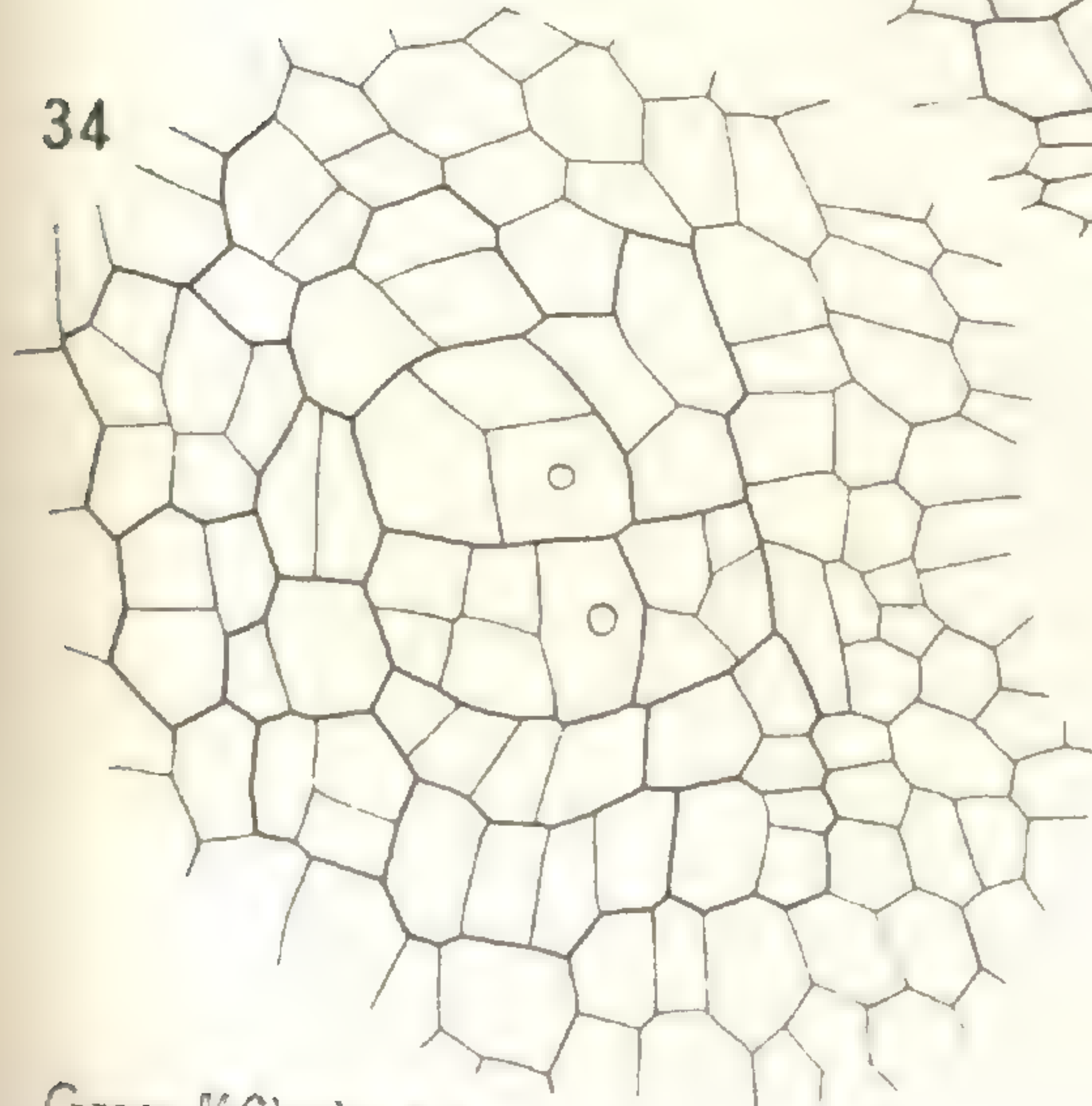
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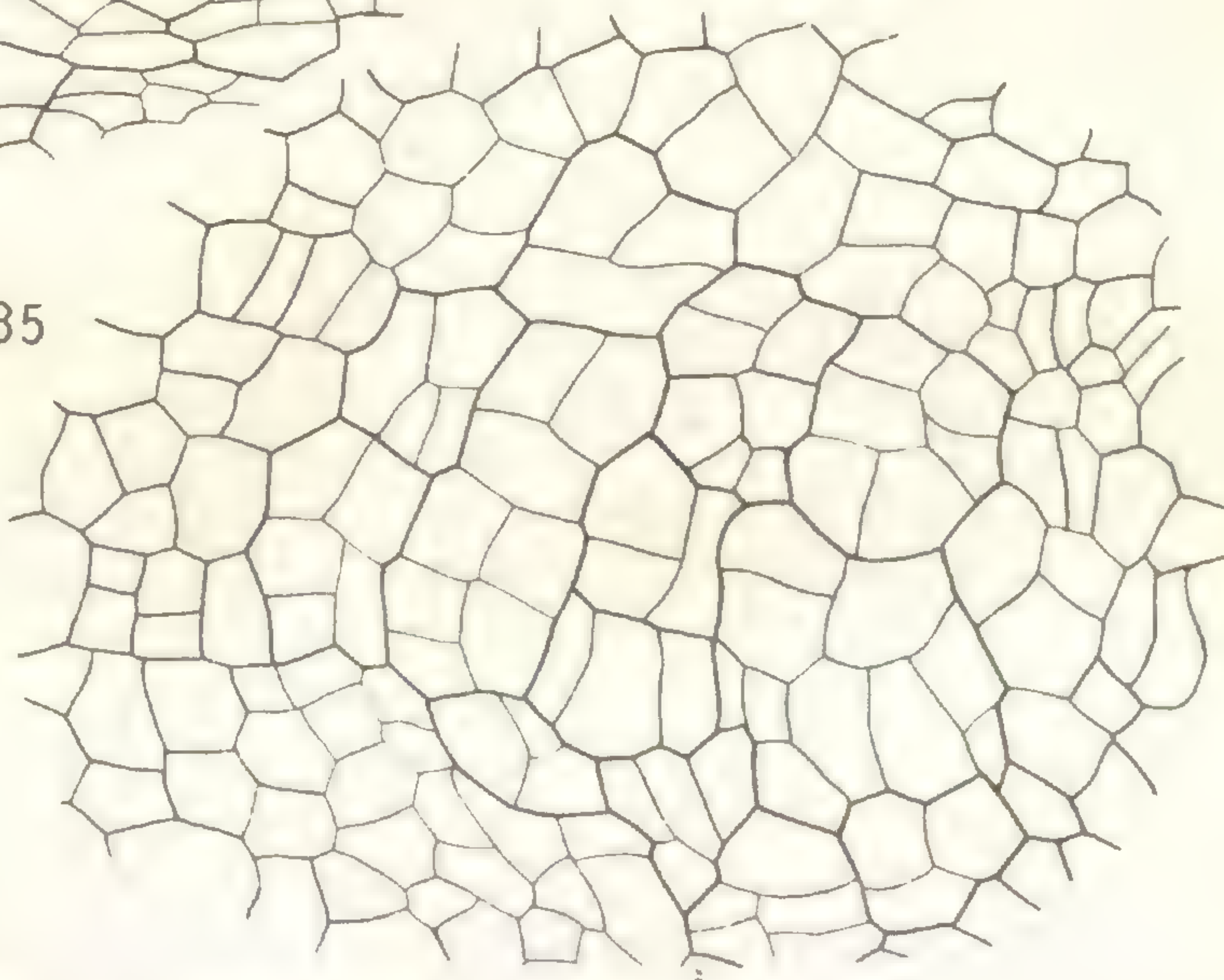
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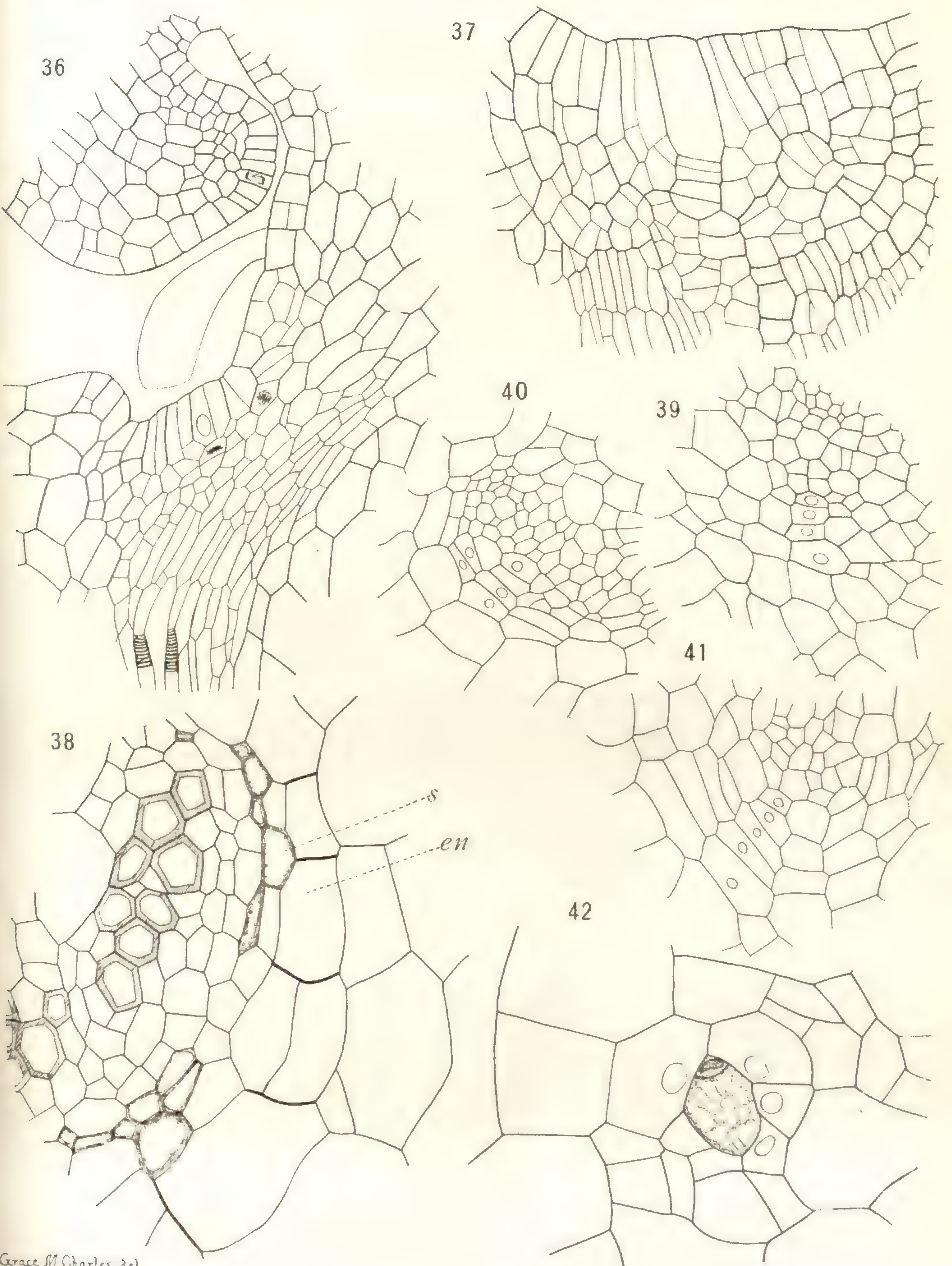
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FIG. 23.—Origin of the medullary strand from the inner surface of a strand of the dictyostele. $\times 188$.

FIG. 24.—Diagram of the strand of the dictyostele at fig. 23, showing the relation of the origins of medullary strand and root trace.

FIG. 25.—Diagram of the vascular cylinder, showing the relation of the medullary strand to leaf gaps and leaf traces.

FIG. 26.—Transverse section of the cotyledonary node, showing the departure of an exarch leaf trace. $\times 400$.

FIGS. 27-30.—Transverse sections of the cotyledonary trace, showing the transition from exarch to mesarch protoxylem. $\times 400$.

FIG. 31.—Transverse section of the apical region of a sporeling with six leaves, showing the triangular apical cell and large segment; at the left above is the youngest leaf trace. $\times 188$.

FIG. 32.—Transverse section of apical region of a sporeling with 25 leaves, showing an irregular apical cell. $\times 188$.

FIG. 33.—Transverse section of an older stem, showing a four-sided apical cell. $\times 188$.

FIG. 34.—Transverse section of a stem 6 mm. in diameter, showing two meristematic blocks of cells. $\times 188$.

FIG. 35.—Transverse section of the apex of a stem 12 mm. in diameter, showing a meristematic region. $\times 188$.

FIG. 36.—Longitudinal section of the apical region of a very young sporeling. $\times 400$.

FIG. 37.—Longitudinal section of the apical region of a stem with 30 leaves; the tissue below the apical cell is pith; at the sides is vascular meristem. $\times 188$.

FIG. 38.—Transverse section of a young stele, showing a frequent relation of sieve tubes to endodermis. $\times 400$.

FIG. 39.—Transverse section near the apex, showing early origin of root from vascular meristem. $\times 130$.

FIGS. 40, 41.—Transverse sections of later stages in the development of roots than fig. 39. $\times 130$.

FIG. 42.—Transverse section of a mucilage duct, showing a cell disintegrating in the mucilage. $\times 400$.

STUDIES ON THE RELATION OF THE LIVING CELLS TO THE TRANSPIRATION AND SAP-FLOW IN CYPERUS. II

JAMES BERTRAM OVERTON
(WITH TWO FIGURES)

Experiments with poisons

In order to kill certain portions of the stems of *Cyperus*, I have used chloroform and ether in the manner described by ROSHARDT, and have always found that the leaves soon droop, behaving exactly like those placed in an atmosphere of these substances. When the fluid is poured into a tube incasing the stem or placed on cotton in the tube, the leaves soon droop. This indicates in my opinion that these substances are soon absorbed and carried to the leaves. The leaves soon fade and wither after treatment with ether or chloroform. I have also made several experiments with xylol in the same way, and found that the results are similar to those obtained by using steam. In one experiment xylol containing eosin was poured into an incasing tube inclosing 15 cm. of a stem 43 cm. high. That the xylol was absorbed by the stem was indicated by the color; at the end of 30 min. the xylol was drawn off and the joints were secured. A plant had been chosen which had a well-developed branch from the base of one of the crown leaves. The involucre remained fresh and turgid for 10 days and then dried, while the branch lived 5 days longer; the part treated with xylol collapsed and the leaves became yellow and dried in about 15 days. The whole behavior of the plant was like that of one which had had a portion of its stem steamed, except that leaves on such steamed plants do not always turn yellow. Other experiments with xylol gave similar results.

I have tried several other poisons in solution, killing 5-10 cm. of the stems by pouring the liquid into incasing tubes. In many cases I have chosen plants with branches developing from the crown. I have used 95 per cent alcohol, 1 per cent chromic acid, saturated

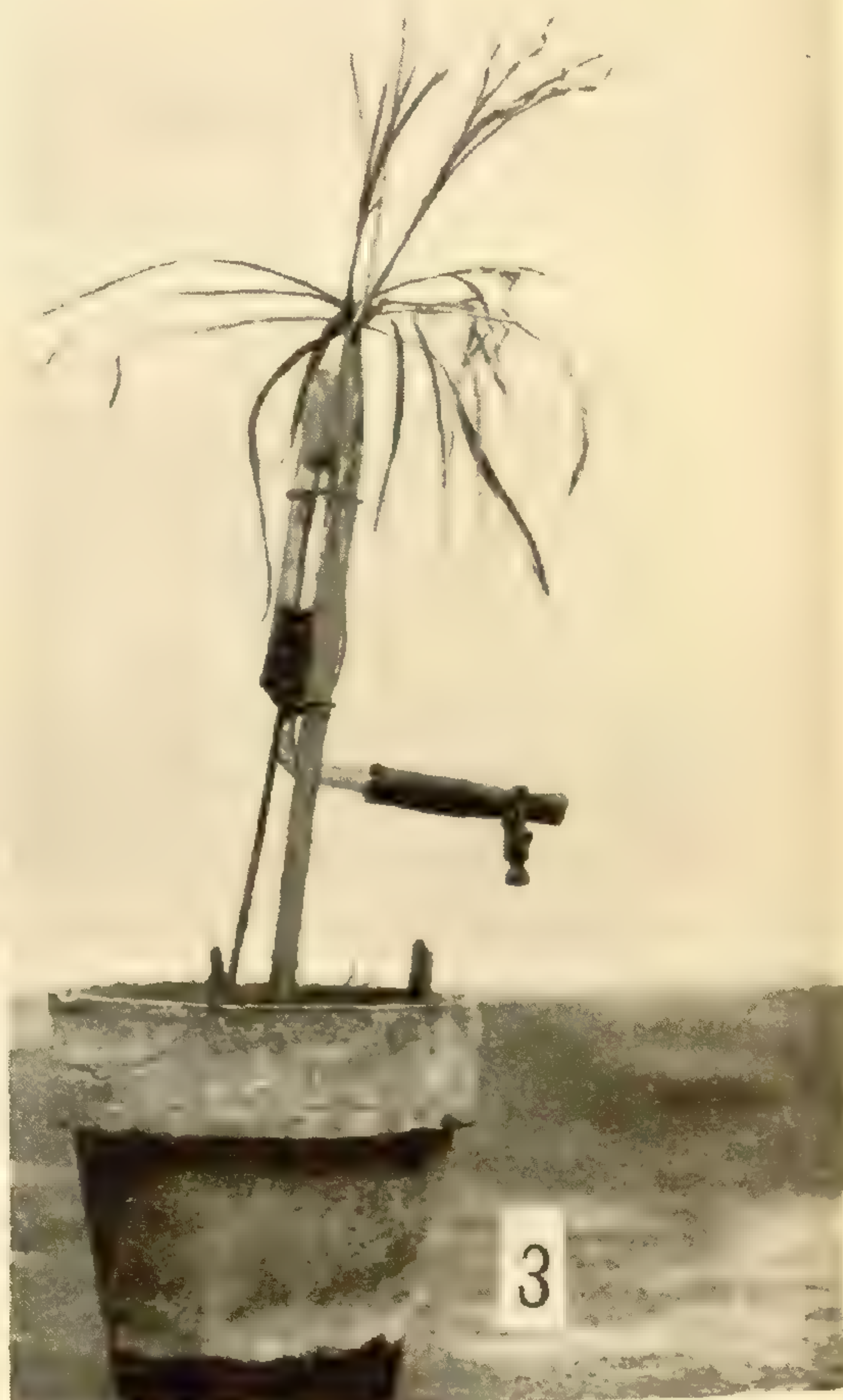
aqueous solutions of HgCl_2 , CuSO_4 , and picric acid, Zenker's fixing fluid, KOH, and 40 per cent formalin for 0.5–72 hours.

In one case 10 cm. of a 40 cm. stem were surrounded for 48 hours with picric solution; the involucral leaves drooped in 3 days, but were perfectly turgid and did not become discolored and dry for 26 days, and the branches, which were 10 cm., 11 cm., and 12 cm. long, remained fresh for 44 days. The incasing tube was then removed and the plant was apparently in good condition. The stem was obviously dead, the immersed region being discolored, but there was no contraction of the protoplasts observable. Other experiments with picric acid are described in table X below.

In experiments with chromic acid, HgCl_2 , Zenker's fluid, formalin, and KOH, the plants very soon faded, although not always losing the turgidity of their leaves immediately after treatment.

By using 95 per cent alcohol and CuSO_4 I have obtained some striking results. On April 12 a plant 35 cm. high, with four branches on the crown, was chosen and the stem incased in a glass tube; 95 per cent alcohol was poured into the tube so as to immerse the stem for 9 cm. The lower portion of the treated region was slightly mechanically injured, so that the alcohol could be readily absorbed; that it was absorbed was shown by a lowering of the fluid in the tube. At the end of 48 hours the leaves of the crown had shown signs of drooping and the liquid was removed; after 7 days the crown leaves and two branches were partially withered. Six of the crown leaves faded and yellowed in 10 days, one branch showed one leaf, and one branch showed 2 leaves alive for 6 weeks. The remaining crown leaves continued green, with but portions yellow, and the remaining 2 branches kept on growing, and at this writing (July 18), after 76 days, were 6 and 8 cm. long respectively, having grown about 5 cm. each. Furthermore, 10 days after treatment, 7 new branches started, all of which were growing (July 18). The incasing tube was removed from the stem, and it was examined to be sure a section was dead. As to this there can be no question, as is shown by the photograph (fig. 2). As a result of this examination, it was found that 4 cm. of the stem where injured were entirely brown and the parenchyma disorganized, which appears black in the figure, but apparently no substance had been carried into the

lumina of the vessels. No streaks could be observed above the dead part, as is the case in stems on which steam is used. Apparently



FIGS. 2, 3.—Fig. 2, photograph of a plant which has had a portion of the stem killed with 95 per cent alcohol; stem split lengthwise in order to show the appearance of the dead portion; dead cells appear black in photograph; parenchyma cells almost entirely disintegrated; this figure also shows the healthy crown of leaves and several new branches which have developed since the treatment and which were still growing at the time when the stem was cut; fig. 3, photograph of a plant 63 days after 10 cm. were killed with CuSO_4 ; incasing tube into which the poison was poured still in place; darkened, shriveled stem seen through glass tube surrounded with a plug of cotton; crown shows several leaves still in good condition and the growing branch in center still turgid.

the plant would have remained alive and the stem have continued to conduct sap as long as the injured portion was protected. The dead portion fell to pieces when exposed and touched. From this

experiment, therefore, it seems possible to kill a certain region of the stem without injuring the leaves, and to show that the dead portion is capable of water conduction so long as actual breaking up can be prevented.

The objection may be raised that the killed region in the above experiment was too short to show conclusively that living cells are not necessary for sap-flow. I have succeeded in killing 10 cm. of the stem by another poison without injury to all of the parts above, and thus obtaining results quite as striking. A stem 23 cm. long, with a healthy crown of 11 involucre rays with 2 branches each 8 cm. long and 2 others each 10 cm. long, was surrounded for 4 cm. with a saturated aqueous solution of CuSO_4 for 36 hours on May 7. The CuSO_4 was absorbed and the stem discolored for 20 cm., or up to the base of the crown. The liquid was removed and a plug of cotton put loosely about the stem in the tube inclosing the upper portion of the 10 cm. which was discolored. On May 20, or after 13 days, the plant was in perfect condition except one branch, some of whose leaves were drying, and the leaf tips of the crown, which showed signs of yellowing. This branch and one of the others finally dried and died, and 3 leaves of the crown died, but the remaining 8 leaves of the crown and the branch have remained perfectly fresh, green, and turgid up to the present writing (July 18); the other branch has grown several centimeters. The stem is partially collapsed, as indicated by its smaller size, and has colonies of mold (*Penicillium*) on it, owing to the fact that the incasing tube was not closely sealed. The stem is dark brown, almost black, and is certainly dead. This experiment shows, therefore, that it is possible for 10 cm. of a dead stem to conduct water for 8 leaves and 2 branches for an indefinite period of time. A photograph of this plant is shown in fig. 3. The results of the above-described experiments appear below in tabular form.

From these experiments with picric acid, alcohol, and CuSO_4 , we see that it is possible to kill a portion of the stem without completely disorganizing the killed stretch and without interfering with its conducting capacity.

I have further attempted to determine quantitatively the amounts of water that may be evaporated from perfectly dead

TABLE X

SHOWING THE EFFECT OF POISONING 4 TO 15 CM. OF THE STEM WITH XYLOL, PICRIC ACID, ALCOHOL, OR CuSO_4

No. of exp.	Height of stem	Distance treated	Time of treatment	Method of treatment	Date	Results and remarks
1—P (1910) . . .	43 cm.	15 cm.	30 min.	Xylol (and eosin)	April 14	Plant and well-developed branch; involucre remained fresh and turgid for 10 days and branch for 5 days longer; whole plant behaved as though it had a portion of stem killed by steam; part in tube collapsed and portion killed; leaves yellowed and dried in 15 days.
4—P (1910) . . .	40 cm.	14 cm.	72 hrs.	Picric acid	April 17	Leaves remained fresh for 7 days; on 8th day leaf tips began to droop, but no signs of withering or fading; plant cut off for examination, acid apparently penetrated stem and carried short distance above place of treatment, but not in leaves, as was shown by color.
5—P (1910) . . .	35 cm.	4 cm.	48 hrs.	Picric acid	May 3	Plant had healthy crown and one large branch from the crown, 10 cm. long and 2 cm. high; crown leaves drooping in 3 days but turgid and green, showing no fading; May 27, no visible withering or fading; plant cut off and examined; no plugging of the vessels or collapse of parenchyma cells.
6—P (1910) . . .	40 cm.	10 cm.	48 hrs.	Picric acid	May 3	Plant had good involucre and 3 branches, one 10 cm., one 11 cm., and one 12 cm. long; in 3 days crown leaves slightly drooping, but perfectly turgid; plant still in good condition June 16; removed for examination (see text description).
2—P (1910) . . .	35 cm.	9 cm.	48 hrs.	95 per cent alcohol	April 12	Plant had 4 branches on crown; crown leaves and 2 branches partially withered in 7 days; in 10 days 6 of crown leaves entirely faded; one branch dry in 10 days; one branch kept one leaf, and one branch kept 2 leaves turgid for 6 weeks; in 10 days after treatment 7 new branches started and were still growing June 18, or 76 days after treatment; stem in tube brown and apparently dead, but not collapsed; cut off for examination; stem fell to pieces where killed.
11—P (1910) . . .	23 cm.	10 cm.	36 hrs.	Saturated aqueous solution of CuSO_4	May 7	Plant had good crown with 2 branches, each 10 cm. long, and 2 others each 8 cm. long; May 15, plant in perfect condition except leaf tips very slightly yellowing; all branches normal; May 20, plant in good condition except one branch; July 9, remaining branches in good condition and growing; July 12, one of remaining branches withered.

plants. It was at once found that the kind of poison used to kill the plant very greatly influences the amount of water evaporated, and that in many cases the amount of water evaporated greatly exceeds the amount transpired by a living plant of the same size and under the same conditions. Cut stems were placed in chromic acid, picric acid, and HgCl_2 for 24 hours, until it was certain from their appearance that the poison had been carried to the leaves and that the whole plant was killed; they were then transferred to distilled water. All of the plants in table XI had 17 leaves, each of the same size, age, and area. The area of each plant in table XII was about three times that of each of the plants in table XI, 21 large leaves being on each. Plants of approximately the same leaf areas and of the same stage of development were chosen for controls. The amount of water evaporated from each plant was determined by weighing. Tables XI and XII give the results of my experiments on this point.

TABLES XI AND XII

SHOWING VARIATIONS IN THE DAILY AMOUNTS OF EVAPORATION FROM PLANTS COMPLETELY KILLED BY CHROMIC ACID, PICRIC ACID, OR HgCl_2 , AS COMPARED WITH A CONTROL PLANT IN WATER

TABLE XI

No. of plant	Fluid	Loss per day in grams										Average loss per day	Percentage of water in plant on 10th day
		1	2	3	4	5	6	7	8	9	10		
I ..	H_2O	0.1	0.9	0.6	0.5	0.5	0.5	0.1	0.4	0.3	0.5	0.44	81
II ..	Chromic	0.1	0.9	0.8	0.8	0.9	0.6	0.5	0.7	0.9	0.5	0.67	36
III ..	HgCl_2	1.2	1.1	1.7	1.6	1.5	1.1	0.8	0.9	1.1	1.3	1.23	28
VI ..	Picric	0.7	0.5	0.4	0.4	0.5	0.6	0.4	0.4	0.2	0.4	0.45	11

TABLE XII

No. of plant	Fluid	Loss per day in grams										Average loss per day
		1	2	3	4	5	6	7	8	9	10	
I	H_2O	7.4	5.1	3.0	0.9	0.6	0.6	*	*	*	0.5	1.8
II	Chromic	2.6	2.9	2.7	2.4	2.5	2.5	*	*	*	3.4	1.9
III	HgCl_2	7.0	7.6	7.0	6.6	6.5	6.5	*	*	*	10.4	5.2
IV	Picric	2.5	1.1	2.7	0.9	2.6	1.8	*	*	*	4.4	1.6

*Impossible to take readings on these days, but does not affect average.

The stems were cut off under water and allowed to remain there for 6 hours, after which they were quickly transferred to the poisons; in each case the base of the stem was immersed for a distance of 5 cm. They were then transferred to bottles containing distilled water, which was covered with a layer of olive oil to prevent surface evaporation. Weighings were made daily at noon for 10 days.

It will be seen from these tables that more water is evaporated from a perfectly dead stem of *Cyperus*, killed with chromic acid, picric acid, or HgCl_2 , than from a cut plant set in water and kept under the same conditions. These substances in some way apparently alter the constitution of the plant so as to allow it to give off more water. As shown by these tables, a plant cut under water and kept standing in water continually falls off in the amount of water transpired from day to day, and very seldom increases the quantity given off on a certain day over that transpired the previous day. In the case of poisoned plants the reverse is true. Noting the plants numbered II in each table, an increase over the first day is shown on each of the two succeeding days. The amount of water evaporated on the 8th and 9th days exceeds that of the 7th. Certain other days show increases over the preceding days. The plant killed with HgCl_2 gives off a quantity of water far in excess of that given off by plants killed by the other two poisons. In table XI plant no. III gives off nearly three times as much water on the average per day as does no. I. Another noticeable fact is that although these poisoned plants evaporate comparatively large quantities of water, the percentage of water contained in the plant is very much below that in plants which have not been killed. This is shown in the last column of table XI; the plant in water contains 81 per cent of water, while the one killed with HgCl_2 , which gave off the largest quantities of water, contained only 28 per cent of its dry weight of water.

General discussion

As shown by BOEHM (3), STRASBURGER (30), URSPRUNG (32-37), DIXON (9-12), ROSHARDT (24), and my own experiments, the leaves above a steamed or otherwise heated portion of the stem

being kept in connection with the roots remain for a considerable period turgescient, but sooner or later wither and die. This is very distinctly shown in table IV, from which data it was concluded that the leaves above a steamed portion never remained longer than 18 days without withering. This was shown to be true when only 5 cm. of the stem were steamed, while the leaves remain turgid for 3 days only when 30 cm. were killed. It has been shown that in *Cyperus* sufficient water to maintain the turgidity of the leaves for 3-18 days will rise through a stem 15-60 cm. high with a section 5-30 cm. long, which has been killed by steam. It has also been shown that sufficient water to keep the leaves turgescient for 3 months can ascend through a stem 23 cm. high when 10 cm. are killed with CuSO_4 . It follows from my observations that the leaves wither above a longer heated stretch faster than above a shorter one, as has been observed by JANSE, URSPRUNG, DIXON, and ROSHARDT. It is further evident that when short portions of the stems are steamed (5-10 cm.), the leaves above do not wither quite as quickly as those on stems cut from the same plant and placed in water under the same conditions of light, temperature, and air moisture. Leaves cut and not placed in water always lose their turgidity and dry long before those on steamed stems, regardless of the length of the killed portion. Such cut branches lose their turgidity in 1-2 hours, and become completely dry in 24-48 hours. The fact that the leaves on heated stems remain longer turgid than those cut and left in air shows that a certain amount of water passes through the killed portion, as is also admitted by URSPRUNG. This is also clearly shown in a quantitative way, by comparing the transpiration after killing a certain portion of the stem with steam with that before the steam was applied. Such a comparison is brought out in tables V and VI. The amount of water passing through such a steamed stem rapidly diminishes, falling off almost immediately from 80 per cent to 50 per cent of the dry weight of the leaves, until the leaves become air dry, when they still contain about 11 per cent of the dry weight of water.

URSPRUNG's conclusion from such experiments, that living cells are necessary for sap-flow, is certainly not obviously necessary. The long period during which the leaves remain turgid in his own

experiments certainly suggests that the death of the stem cells does not operate in any direct fashion to cut off the water supply. Such a period as 18 days gives opportunity for the development of all sorts of secondary causes, to which the final death of the leaves may well be due. That the amount of water carried is at once reduced may just as well be due to gross mechanical changes secondarily produced in the tissues as to the death of the cells.

DIXON calls attention to the fact that the investigators who first observed the withering of the leaves above a heated portion of the stem, such as WEBER (40) and JANSE (16), did not attribute the phenomenon simply to the lack of activity of the dead cells of the stem, but to a possible blocking of the vessels, which thus diminishes the water supply. It is certain from the methods which I have used to protect the steamed portions of the stems, that the diminished water supply which reaches the leaves after treatment cannot be due to a lateral evaporation from the heated stretch. The carefully sealed incasing glass tubes preclude such a possibility. URSPRUNG has also concluded from his experiments that the wilting of the leaves above a killed portion of the stem is not due to a lateral evaporation from the heated portion.

In the experiments whose results are shown in tables VIII and IX, there was an increased amount of water transpired on certain days after a section of the stem was killed with heat. It appears, therefore, that URSPRUNG's statement that the fading of the leaves above a killed portion is a sure index that insufficient water supply reaches them is not proven, and that the wilting may well be due to deleterious substances being introduced into them from the dead cells. Although the plant described in table IX had an increased amount of water ascending to the leaves, they finally withered while still giving off large quantities of water. I am forced to agree with DIXON (10-12) that URSPRUNG's interpretation of these phenomena is an arbitrary one. As noted above, DIXON ascribes the earlier wilting of the leaves on stems, a section of which has been killed with heat, to a possible clogging of the vessels, which hinders water passage, or to a breaking of the water columns due to the heat used, which may thus interrupt the continuity of the flow. He holds, however, that the withering of the leaves is due chiefly

to the action of poisonous or plasmolyzing substances in them, which interferes with the osmotic action of the cells and thus inhibits their lifting power. URSPRUNG regards this suggestion as an empty conjecture.

My results agree well with those of ROSHARDT, except that in the plants treated with steam I have never observed an increase in the amount of water given off during any one period over that in the preceding, such as is shown by ROSHARDT's table. It appears to me that if the living cells of the stem are necessary to the ascent of water, as ROSHARDT contends, there could not possibly be an increased amount of water transpired during any one interval over that of the preceding. The general gradual falling off in the amount of water transpired after killing a portion of the stem, which ROSHARDT records, agrees with my observations on *Cyperus* under similar circumstances, except that the diminution in the amount of water lost, after steaming a section of the stem, is continuous. I feel that the cause is the same in both cases, namely, a stoppage of the vessels, which I have actually shown to occur in *Cyperus*, and a probable injury to the leaves due to deleterious substances being introduced into them. It seems to me that ROSHARDT has placed exactly the opposite interpretation on the results of his quantitative experiments to that which they really show.

Microscopical examinations of the stems of *Cyperus* above a steamed stretch show that some of the vessels are plugged for a considerable distance with a brown, gumlike gelatinous mass, which reacts to alkanin like resin. This substance is insoluble in water and often stops the vessels throughout the length of the stem above the killed portion, even plugging some of the tracheae of the leaves. There can be no doubt that this stoppage of the vessels in *Cyperus* accounts in a large measure for the immediate and constantly diminished water supply which reaches the leaves above a steamed portion of the stem. The discoloration of the contents of the sieve tubes is conspicuous, and suggests that the steaming causes considerable disorganization, which may be the source of the resinous substances in the vessels. Although URSPRUNG observed stoppage in several plants, he thinks that the

diminished water supply cannot be due to this, since the leaves do not wither at once, but remain for some time turgid. I have described the progressive effect which steaming the stems of *Cyperus* has on the withering of the leaves, but I attribute this progressive injury, which finally results in the death of the leaves, to the introduction of injurious substances from the dead cells. The presence of these poisonous or plasmolyzing substances seems to account for the final withering or drying of the leaves. The leaves first die and then dry, as DIXON puts it. The leaves do not die from lack of water supply, as URSPRUNG would have it, but because they are killed.

Not only are the cavities of the vessels plugged with a brownish mass, but the walls of the conducting tubes are tinged with yellow. It seems quite probable that the presence of some substance in the walls of the tubes may lessen their power of conduction also. DIXON (10-12), as noted, has observed the presence of a substance which stains the walls of the vessels and thinks that "it would be hard to believe that the deposit of this colored substance in the walls and lumina of the tubes could be without effect on their efficiency in transmitting water." I have already described a similar brownish appearance of the walls of the vessels as well as the plugging of the lumina for some distance above the cut end of a stem of *Cyperus* standing in a sterilized decoction of the same plant. SCHWENDENER'S (28) researches, tending to show that heating the stem does not change the physical character of the cell walls of the tubes, and that the micellar structure and imbibitional power is not affected by such treatment, probably do not take sufficient account of the action of poisonous substances caused by heating the stem on the structure of the walls of the vessels and the efficiency of their conductivity. From my experiments it is clear that changes in conductivity and in the amount of evaporation are brought about by killing the plant with such substances as chromic acid, picric acid, and HgCl_2 , often accelerating evaporation to a very marked degree.

I have repeatedly shown that when stems are set in a decoction of the same plant, the leaves wither much earlier than those set in water. Additional evidence that injurious substances are engendered by heating the plant was obtained by growing *Cyperus*

plants in nutrient solutions containing a decoction. As noted above, the plants grown in such solutions began to droop in 3-5 days, showing discoloration and fading along the veins in 7-8 days, while control plants grown in nutrient solutions without the decoction remain perfectly normal. DIXON's experiment, in which leaves normally supplied with water together with water from a heated side branch were shown to soon wither, seems to me quite decisive proof that deleterious substances enter the leaves from the killed portion. URSPRUNG (35-37), however, was unable to produce the same effect on the leaves of *Impatiens* by using DIXON's method.

Microscopical examination of the leaves from a stem killed by heat show in certain regions a discoloration of the mesophyll cells, the protoplasts being contracted and the chloroplasts being discolored. The leaves of plants grown in decoctions also show similar conditions. DIXON (10-12) also found disorganization and discoloration of the mesophyll cells of the leaves above a killed portion, and, as noted, even on a separate branch if some of its water supply passes through a heated region. In these cases it certainly appears that the leaves are drying not so much for lack of water as from injury and death of the cells. The observation of SCHROEDER (27) that most leaves can lose 50 per cent of their fresh weight without injury is further proof that leaves above a heated portion of a stem do not wither on account of the diminished water supply. In the microscopical examinations which I have made of leaves from steamed stems, I have found many of the conditions described by SCHROEDER in his studies on the symptoms of death as a result of wilting, namely, the contraction of the protoplasts of the mesophyll, and the change in color and rounding up of the chloroplasts. The fact that the plant killed with steam constantly decreases in the amount of water given off is also in harmony with SCHROEDER's observations. The first 50 per cent of the leaf's fresh weight is very rapidly lost when dying, as he shows, after which the amount lost decreases uniformly. My experiments, in which the amount of transpiration was determined after killing a portion of the stem with steam, show that there is in the first 2 or 3 days a very rapid and immediate decrease in the water loss, and that then the rate of transpiration

decreases more uniformly. These facts, taken together with the appearance of the mesophyll, seem to show beyond question that the leaves on a steamed stem are dying, and that death is not entirely due to a lack of water.

Applying heat by means of wax heated to 110° C. does not cause so much discoloration of the contents of the sieve tubes, or so much stoppage of the lumina of the vessels, and the mesophyll of the leaves does not show so much immediate plasmolysis. The leaves above stems so treated remain turgid three times as long as those on steamed stems. Plants do not show such an immediate decrease in the transpiration as is the case when the stems are killed with steam. The effect upon the transpiration rate and upon the injury to the leaves in using hot wax is not a progressive one, as it is when steam is used. Altogether the method of using hot wax to kill a section of the stem seems more satisfactory than steaming, with reference to the question of the relation of the living cells to sap-flow. And it is still plainer in stems killed in this way that the death of the stem cells does not *per se* directly affect the sap-flow.

My experiments with poisons, in which 5–10 cm. of the stem were treated for 36–72 hours, show that it is possible to kill a portion of the stem without completely disorganizing the killed stretch and without reducing its conducting capacity. Not only does a sufficient quantity of water pass through the poisoned portions to supply the transpiration needs for a comparatively long period of time (3 months in the case of CuSO_4), but also to allow the development and growth of new parts. As has been shown, the mesophyll cells remain perfectly normal; no discoloration of the chloroplasts and no contraction of the protoplasts follow this method of treatment, if care is taken that the poison does not reach the leaves. In the poisoned portion of the stem the cells are apparently “fixed” when alcohol or picric acid is used, there being no plasmolysis. When CuSO_4 is used, the parenchyma of this region has its protoplasts contracted, but the vessels remain normally open and apparently unaltered.

From my experiments, in which poisons were used to kill the whole plant, it was at once evident that the kind of poison greatly influenced the subsequent rate of evaporation of water from the

whole plant, and that in many cases the new rate far exceeds the normal transpiration of a plant of the same age and superficial area under the same conditions. In these cases it is plain that the tissues are ruptured so as to expose additional cell surfaces to the atmosphere.

DIXON and JOLY (13) consider that capillarity or imbibition of the mesophyll cell walls sets up a suction, aiding the osmotic suction in extracting water from the adjacent vessels. In the case of the poisoned leaves of *Cyperus* there can be no osmotic action of the cells. The imbibitional action of the cell walls, as conceived by DIXON, may however still keep the walls wetted, and the suction from the evaporation may be transmitted to the cohering water columns of the vessels. DIXON (11) points out that the point of support for the tensile strength in the case of transpiring dead organs is always the walls. He thinks that the presence of soluble substances on the outer surface of the walls would function also in maintaining the suction. Perhaps the condensation of the metallic salts of these poisons on the outer surfaces of the cell walls act in this manner.

BOEHM (4) formulated a theory of sap-flow based entirely upon capillarity, maintaining that the capillary attraction between the walls of the conducting tracts and the water is greater than obtains in a glass tube of the same diameter. The experiments of STRASBURGER (30), however, show that in the vessels of *Aristolochia* the capillary ascent of water is much slower than in glass tubes of the same diameter. It seems quite possible that HgCl_2 , and some of the other poisons used by me, which cause an increased amount of evaporation, as is shown in tables X and XI, may in some way alter this capillary relation so that the water may flow faster in such poisoned tubes. Cells without turgor, that is perfectly dead cells of the leaves, are able to raise water to a considerable height. STRASBURGER showed that rather tall trees with poisoned leaves are able to raise water 22 m. ASKENASY (1) found that cut branches of *Taxus* and *Viburnum*, whose lengths he does not mention, which had lain for a long time in boiling water or in alcohol and were completely dead, could suck up water and eosin. BOEHM (4, 5) also showed that water could rise in a dead

branch when the leaves were dead. A cooked and dried oak twig about 25 cm. long was then set in a tube with a manometer, with water above and mercury below. The twig was able to raise mercury 70.3 cm. high. In another somewhat modified experiment with a *Thuja* twig the mercury rose to 86.4 cm.

ASKENASY believes that the suction power exhibited by dead leaves is explainable by the fact that the water evaporates from the outer surface of the cell walls of the mesophyll into the intercellular spaces, and is supplied from within through the protoplasmic lining. He thinks that the imbibitional force of the wall is greater than the osmotic power of the cell sap. He further adds:

Da diese Imbibitionskraft durch den Tod der Zelle im Allgemeinen nicht beeinträchtigt wird, so ist es kein Wunder, dass auch tote Zellen, wenn sonst die Verhältnisse günstig liegen, im Stande sind, das an ihnen verdunstende Wasser ebenso hoch zu heben wie lebendige.

There can be no doubt that cell walls possess a great attraction for water. As DIXON (10-12) points out, the submicroscopical spaces occupied by the imbibed water in the cell walls of the mesophyll are intensely minute capillaries. It seems quite possible that these poisons may in some way alter the character of these passages, and so affect the amount of water imbibed by the walls and also the amount of water evaporated by the surfaces of these cells. It is certain that in the case of plants poisoned throughout, the elevation of the water in the stems, and its evaporation from the leaves in larger quantities than normally occurs in living plants, depend purely upon physical processes.

Summary

1. Stems of *Cyperus* cut and placed in water wither sooner than when a certain portion, not to exceed 20 cm., has been killed by steam.

2. When 20 cm. of the stem are killed by steam, the leaves wither in about 8 days, that is, in about the same time as the control plants.

3. The longer the portion of the stem killed with steam, the sooner the leaves above wither and dry. When 25 to 30 cm. of the stem are killed with steam, the leaves wither in 3-5 days.

4. No matter how long the section killed may be, the leaves on steamed stems never wither quite so quickly as those cut and not placed in water, but under the same conditions of light, temperature, and air moisture.

5. In *Cyperus* sufficient water to maintain the leaves turgid for 3-18 days will rise through a stem 15-60 cm. high, with a section 5-30 cm. long which has been killed with steam.

6. A certain amount of water is raised through the steamed portion, but it gradually diminishes in quantity from day to day, until the leaves become air dry (about 11 per cent of their dry weight of moisture).

7. The diminished water supply is partly due to a partial blocking of the vessels with a gumlike or resinous substance, which probably owes its origin to the disorganization of the contents of the sieve tubes caused by heating the stems.

8. The withering of the leaves above a steamed portion of the stem is probably caused more by the action of deleterious substances introduced into them from the dead cells than from lack of water. These poisonous substances are probably disorganization products caused by heating with steam.

9. The leaves of rooted plants, grown in nutrient solutions containing sterilized decoctions of the same plant, droop in 3-5 days, discolor and dry in 7-8 days.

10. The withering leaves above a portion of the stem killed with steam show all the symptoms of dying, namely, rapid loss of water after treatment, then a more uniform loss, rounding up and discoloration of the chloroplasts, and contraction of the mesophyll protoplasts. The leaves are apparently drying, not so much from lack of water as on account of the death of the cells from other causes.

11. Judging from the behavior and disorganization of the leaves on a stem, a section of which has been killed with steam, it is evident that this method of killing the cells is not a satisfactory one in order to settle the question as to the relation of the living cells to sap-flow.

12. Killing a portion of the stem by applying wax heated to 110° C. causes less apparent disorganization of the cells, less injury

to the leaves above, and does not cause a marked immediate decrease in the transpiration.

13. Experiments in which 5-10 cm. of the stem are killed by treatment with picric acid, 95 per cent alcohol, or CuSO_4 , for 36-48 hours show that sufficient quantities of water may ascend through the poisoned portions to supply the transpiration need for a comparatively long period (90 days), and to allow the development of new branches.

14. Certain poisons (picric acid, chromic acid, and HgCl_2) may greatly accelerate the amount of water evaporated in poisoned plants. Not all poisons act alike in this respect; HgCl_2 causes the greatest amount of increase in water loss.

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REDUCTION BY ROOTS¹

OSWALD SCHREINER AND M. X. SULLIVAN

The roots of many plants, such as wheat, have an oxidizing power (1). This property is readily shown by certain chromogens, alphanaphthylamine, benzidine, phenolphthalin, aloin, guaiac, pyrogallol, etc. When chromogens like alphanaphthylamine and benzidine are used, the colors due to oxidation are shown on the root itself. The most marked oxidation is shown by a narrow but very distinct band of color just back of the root cap. Then comes a practically colorless zone and then a broad colored zone, the color becoming less intense toward the upper part of the root.

In regard to the practically colorless zone or the zone with little color just back of the region of intense coloration, it seemed as if the lack of color might be due to a reducing power, a reductase or possibly an antienzyme.

The possibility of an antienzyme is suggested by the work of BERTEL (2), who showed that with the exclusion of oxygen there accumulated in the cells of the lupine roots larger quantities of tyrosine than are usually found. The tyrosine which arises from the protein degradation in the early stages of the seedling's growth is normally oxidized by the enzyme tyrosinase to homogentisic acid and oxidation products of the latter. With the exclusion of oxygen, this oxidation is retarded and tyrosine accumulates.

Subsequently CZAPEK (3) showed that "a short time after the beginning of geotropic induction there appears a retardation of the normal destruction of tyrosine to be recognized by an accumulation of homogentisic acid." The cause of this retardation he attributed to the development of specific antiooxidase which inhibits the normal activity of the oxidase of the root tip.

Reducing properties have been found in animal organs, in microorganisms, and in plant juices. The reducing power of the animal organism was shown first by EHRLICH (4), who used alizarin

¹ Contribution from the Laboratory of Soil Fertility Investigations. Published by permission of the Secretary of Agriculture.

blue and the more easily reduced indophenol blue, both of which on reduction give colorless bodies. On injecting these colored substances he found that organs of the animal could reduce them to the leuco-bases. EHRLICH divided the organs of the body into three main groups: (1) those highly saturated with oxygen in which indophenol blue remains; (2) those in which indophenol blue, but not alizarin blue is reduced; (3) those of highest oxygen avidity, in which alizarin white is formed.

In the first group are the gray matter of the nervous system, heart, part of the muscular system, and kidney capsule; in the second group, most of the muscular system, glands, and connective tissue; in the third group, the lungs, liver, fat, Harder's gland, and mucosa of the stomach.

Since EHRLICH's experiments, the reducing power of animals, plants, and microorganisms has been extensively studied. The reagents used to demonstrate the reducing power are numerous. Among them are various colored substances which form leuco-bodies, such as lacmus, methylene blue, indigo carmine, indigo blue, gentian violet, methyl violet, rosaniline, etc.; nitrates, which are reduced to nitrites; sodium selenite and sodium tellurite, which are reduced to metallic selenium and tellurium. Methylene blue and lacmus are used most. The former is converted to a leuco-base by the addition of hydrogen, the latter apparently by the abstraction of oxygen.

Reduction has been studied more extensively in the case of microorganisms than in animals and plants. Whether the reduction produced by microorganisms is due to enzymes or not has not yet been settled. ROZSAHEGYI (5), BAGINSKY (6), MÜLLER (7), and WOLFF (8) believe that the reduction is caused by external metabolic products; while CAHEN (9), SPINA (10), SMITH (11), KLETT (12), MAASSEN (13), and CATHCART and HAHN (14) regard it as an attribute of the bacterial cell. They all agree, however, that the reduction is associated with the development of bacteria.

In regard to reduction in higher plants, it might be mentioned that BINZ and SCHULZ (15) found that plant protoplasm had the power of reducing arsenic acid (As_2O_5) to arsenious acid (As_2O_3), while plant protoplasm treated with boiling water lost this power

to a great degree. REY-PAILHADE (16) extracted from yeast cells by means of alcohol a substance which would form H_2S from S . To this substance he gave the name philothion. He found it likewise in fresh animal tissues, in the tips of young shoots of asparagus (17), and in various grains and young seedlings (18). Pozzi Escot (19) verified REY-PAILHADE's work and succeeded in hydrogenating in addition metallic selenium and phosphorus. PALLADIN (20) found a reductase in wheat shoots and concluded that it played a part in respiration. DELEANO (21) found a reductase or hydrogenase in the albumen of *Ricinus communis*, but not in the roots or the plantules. The albumen triturated with sulphur gave hydrogen sulphide. LAURENT (22) showed that young seedlings reduce nitrates and that there can be extracted from plants an unorganized ferment which has the power to convert nitrates to nitrites. ABELOUS and ALOY (23) found a nitrate-reducing enzyme in potato tubers. KASTLE and ELVOVE (24) confirmed the presence of the nitrate-reducing enzyme in the potato and showed that it was present also in the fruit of the egg plant (*Solanum melongina*). Recently IRVING and HANKINSON (25) have found nitrate-reducing enzymes in certain water plants.

Since little has been done upon the reducing power of seedlings growing in soil or solutions, experiments were made to determine the power of the intact and growing roots, especially of wheat, to reduce substances, with the ultimate purpose of seeing if, like the oxidative power, the reducing power would be found to play a significant part in soil fertility.

Various dyes such as methylene blue, indigo carmine, Bismarck brown, gentian violet, etc., were first employed to see if the roots would decolorize the solution in which they were growing. The color of dilute solutions of the dyes was greatly lightened by the growing roots, especially if air was excluded. Since, however, more or less of the dye-stuff was deposited on the outer surface of the root and root hairs, such solutions were not considered satisfactory for showing reduction if this occurs.

STARCH IODIDE SOLUTION.—When wheat seedlings are placed in dilute solution of blue starch iodide with seeds and roots in the solution, the blue color is soon discharged. With the roots only in

the starch iodide solutions, the color is discharged slowly. The addition of hydrochloric acid to the decolorized solution brings back the blue color. Reducing agents such as sodium thiosulphate, formaldehyde, hydrogen sulphide, etc., behave similarly.

Seedlings were kept in water solution of iodine of 0.012 per cent strength of iodine for two hours with: (a) seeds and roots in iodine solution; (b) roots only in iodine solution; and (c) control in which no plants had been. Solution (a) gave no color on addition of the starch; (b) gave a slight blue color; and (c) gave a deep blue.

On addition of a few drops of concentrated hydrochloric acid, all the solutions became deep blue and no difference could be seen in the depth of color. It would seem then that the plants hydrogenate the iodine, forming an iodide from which the acid liberates the iodine, or that the plants in some way render the iodide inactive toward the starch.

Since the chemistry of the starch iodine combination is not sufficiently known, and since the intensity of color produced by the reaction between starch paste and iodine is by no means quantitative, the effect the seedlings had on this reaction was taken merely as a sign of the possibility of a hydrogenase or a reductase in the seedlings, seed, or root.

SULPHUR.—The roots and the seed and roots of the intact seedling were put in contact with well washed, precipitated sulphur, neutral, made slightly acid with hydrochloric acid, or slightly alkaline with sodium hydroxide. In no case was hydrogen sulphide detected by means of lead acetate paper. Alcoholic extracts of the crushed seedlings after the method of REY-PAILHADE (16), and Pozzi-Escot (19) were likewise found to have no hydrogenating action on precipitated sulphur.

HEFFTER (26) found that compounds containing the sulphydryl or SH group such as thiophenol, benzylmercaptan, ethylmercaptan, thioglycolic acid, and cystein reduce sulphur, and came to the conclusion that the reducing power of cells is due to the labile hydrogen of sulphydryl compounds which give up their hydrogen and become disulphides. This sulphydryl group is present in certain albumins, and is shown by a purple-red coloration with

sodium nitroprusside and sodium or ammonium hydroxide. The crushed wheat roots or seedlings do not give this reaction. According to HEFFTER, non-reducing albumins can be changed to reducing albumins by treatment with a 10 per cent sodium sulphite solution for 12–24 hours and will then give the nitroprusside reaction.

Wheat seedlings of different stages of development from three to ten days old were rapidly crushed, covered with a 10 per cent solution of sodium sulphite, and kept at 40° C., with repeated shaking. The solutions with suspended matter were tested after 2, 6, and 24 hours, and at no time gave the nitroprusside reaction for the sulphhydryl group nor did they reduce sulphur. In 24 hours the seedling pulp was tested for the sulphhydryl group with negative results, and the pulp formed no hydrogen sulphide from freshly precipitated sulphur.

NITRATES.—To test the power of wheat seedlings to reduce nitrates to nitrites, the wheat grains were treated with a 0.1 per cent solution of mercuric chloride for 30 minutes, and the seeds, well washed with sterile water, were placed in sterile tubes containing a little water. In the tubes tightly closed with cotton the wheat germinated and grew well. There were added to each tube 10 cc. of a 1 per cent solution of potassium nitrate, and after 24 hours the solution was tested for nitrites by means of Griess reagents (27), sulphanilic acid and naphthylamine acetate. The ungerminated seeds, whether sterilized or not, did not give the nitrite test under these conditions. The solutions containing the seedlings, on the other hand, gave good tests for nitrites. The ability of sterile seeds germinated in tubes to form nitrites from nitrates was tested several times, both in air and in vacuum. Sometimes a fair amount of nitrite was formed, in one case as high as 6 parts per million, sometimes the amount was very little. It should be borne in mind, however, that nitrites are absorbed by plants. The formation of nitrites was greater in vacuum. It would seem that a nitrate-reducing power appears in the early stages of the wheat seedling, but is not in the seed at rest. The formation of nitrites is small, and no culture tests were made to show that microorganisms were entirely excluded in the experiment. It may be said, however, that enzymes capable of reducing nitrates have been reported in

plant tissue by LAURENT (22), ABELOUS and ALOY (23), KASTLE and ELVOVE (24), and IRVING and HANKINSON (25). LAURENT claims that young seedlings of maize, white lupine, and peas have a reducing action on nitrates, while IRVING and HANKINSON have found that a number of plants reduce nitrates more or less.

SODIUM SELENITE.—Sodium selenite was next employed as a test solution. Solutions of sodium selenite of 0.25 per cent were first used. The solutions reacted alkaline to litmus and phenolphthalein, and were toxic to the young seedling. When neutralized by hydrochloric acid, however, the toxicity of the selenite was greatly lessened. When seedlings were grown in the sodium selenite solution made neutral or slightly acid to phenolphthalein and of a strength of 0.125 to 0.25 per cent, the parenchyma cells of the end of the root cap were colored an intense pink in a few hours, varying with the seedlings, by the deposit of selenium. This deposit was more marked in slightly acid solutions. The points of emergence of the secondary roots were likewise colored. Later the whole root became colored.

SODIUM TELLURITE.—When sodium tellurite is used as a test for reduction, the roots are colored a blue-black by the deposit of metallic tellurium, otherwise its behavior is like that of sodium selenite.

These experiments show conclusively that the intact roots possess a reducing power. This reducing power is stronger in the young seedling, being much stronger in the seedling 4 days old than in the seedling 12 days old. As judged by the quickness with which the deposit of selenium is made on the roots and the extent and intensity of the deposit, the reducing power increases from time of germination to the sixth or eighth day and then decreases. It is still present in seedlings 13 days old, the oldest seedlings examined. The oxidizing power of the wheat seedlings, on the other hand, as judged by the oxidation of aloin, is less in the young seedling and increases with age, being considerably greater in the twelve-day seedling than in the six-day seedling, and still greater than in the case of the four-day seedling.

Dying tissue tends to have a reducing action. The reducing action of the wheat roots on sodium selenite, however, is not a

death phenomenon, since (1) roots killed by being dipped in boiling water have no reducing action on the selenite; (2) the roots in toxic non-neutralized sodium selenite do not reduce; (3) intact roots boiled in solution of sodium selenite have no deposit of selenium upon them; (4) the root ends being cut off and the injured root placed in the selenite solution, the deposit of selenium is not on the cut end but at the point of emergence of the secondary roots.

The reducing power of the wheat roots on sodium selenite is checked by acids and alkalies and by toxic organic matter. It is stimulated by faintly acid reaction and by light. The observable action of salts on the reducing action is variable on account of lack of precision of method, though as a rule sodium nitrate solution equivalent to 50 p.p.m. NH_3 gives the quickest and heaviest deposit at the root tip, while potassium salts give the heaviest deposit on the rest of the root. Potassium salts containing 50 p.p.m. K_2O appeared to retard reduction slightly at the root tip. Potassium iodide containing 14.5 p.p.m. K_2O , however, stimulated reduction.

Incidentally it is of interest here to state that potassium retards greatly the oxidation power as indicated by aloin, and that a slight acid reaction stimulates reduction while inhibiting oxidation, thus seeming to show that the reducing and oxidizing powers are not necessarily concomitant.

Whether or not the reducing power of the wheat roots on sodium selenite is due to enzyme activity, it is hard to say positively. In regard to the enzyme nature of the reducing agent in animal cells, HEFFTER (26) concluded that there were two groups of reduction processes. One group was hardly influenced by hydrochloric acid or by heating. This group embraced the formation of hydrogen sulphide from sulphur, the reduction of arsenic, tellurium, and selenium compounds, the reduction of cacodylic acid and of different dye-stuffs. These reductions he believes are caused by the labile hydrogen of the sulphhydryl group of certain albuminous bodies. The other group of reduction processes, such as the change of nitrates to nitrites and of nitrobenzol to amino combinations, were restrained by heat. This group of reactions he thought at first might be enzymotic, but later he came to the conclusion (26) that they likewise were non-enzymotic.

Whether enzymotic or not, the reducing action on sodium selenite is most marked intracellularly in the parenchyma cells of the root tip. The primary localization of the deposited selenium in the root tip speaks neither for nor against the enzyme nature of the reducing power.

Reduction of sodium selenite may be brought about by purely chemical means. Thus GRÜSS (28) found that lactic acid could precipitate selenium from sodium selenite. Lactic acid we have found to have no reducing action on sodium selenite of a strength of 0.25 per cent, but has some reducing action on a 4 per cent solution of sodium selenite, especially on warming. Citric, tartaric, malic, and oxalic acids do not reduce sodium selenite in the cold, but do reduce strong solutions of the selenite on boiling with a slight excess of the acid. Hydrochloric acid has no reducing action on the selenite solution. Citric, tartaric, malic, and oxalic acids have a reducing action likewise on ferric salts, converting them to the ferrous form. Unsaturated fatty acids such as oleic and elaidic also have the power to reduce sodium selenite and tellurite to metallic selenium and tellurium on warming the mixtures on the water bath. Dextrose likewise reduces the selenite and tellurite on warming. A strong solution of sodium selenite mixed with a solution of invert sugars made by warming cane sugar with dilute hydrochloric acid was completely reduced in the slightly acid mixture on standing 48–72 hours at the room temperature of about 30° C.

JONES (29) injected selenate into the blood of animals. The selenate was reduced to selenite, a small part of which was excreted in the urine. The remainder was carried to the spleen and liver, where it was reduced by dextrose to selenium. When the dextrose was exhausted, fat was called upon. JONES suggests that dextrose is possibly the means by which all reduction processes in the body are brought about. He found that arabinose, glucose, and sugars yielding glucose would reduce sodium selenite on heating, while levulose could reduce it at 30° C. on long standing.

As regards the reduction of sodium selenite and tellurite by wheat roots, it seems probable, since no reducing enzyme could be extracted from the crushed plant, although the juice did show reduc-

tion of selenite upon heating, that the reduction is due to the metabolic activities of the roots, to some unstable non-enzymotic bodies comparable to the oxyorganic acids, which have a slight reducing power, or to complex, unsaturated compounds comparable to dextrose and levulose or the unsaturated fatty acids.

In regard to the significance of the reducing power, it may be said that reduction in organisms runs in general concurrently with oxidation, and is probably just as important an index of life activity. A better medium than sodium selenite is required, however, for a detailed study of this reducing power. Such a medium would be a chromogen which changed color under the reducing action, and thus would present a possibility of estimating the change colorimetrically and quantitatively. The fact stands, however, that the growing root possesses reducing powers.

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STUDIES ON THE PHLOEM OF THE DICOTYLEDONS¹

I. PHLOEM OF THE JUGLANDACEAE

ANSEL F. HEMENWAY

(WITH PLATE XIII)

During the past year the writer has studied the phloem of *Juglans nigra*, *Juglans cinerea*, *Carya ovata* (hickory nut), *Carya alba* (mockernut), *Carya glabra* (pig nut), and *Pterocarya caucasica* (Caucasian walnut). The phloem of some thirty species of other lower dicotyledonous trees has also been investigated in a preliminary way. Next year this research will be continued. A general account of the literature on the subject will be presented in the subsequent paper.

The sieve tubes of the gymnosperms and the vascular cryptogams have sieve plates on their lateral walls as well as on their fusiform end walls; while in the angiosperms true and typical sieve plates are supposed to be confined to the oblique or horizontal end walls of the sieve tube. HILL² states:

The term "sieve field," in the sense in which it is used in this paper, denotes the group of fine connecting threads or strings which are found normally on the lateral walls, and which serve as a means of communication between adjoining sieve tubes. The sieve plates occur on the horizontal or oblique end walls of the sieve tubes, and occasionally on the lateral walls also, but their slime strings are readily distinguished from sieve fields owing to their large size.

The object of the present research was to discover, if possible, any ancestral characters of the phloem, and especially to determine if the sieve tubes of any of the lower dicotyledons had lateral "sieve plates" instead of lateral "sieve fields."

In collecting material, it was found that the pieces of tissue from the main trunk of large trees were most satisfactory. Specimens taken from the trunk near the ground were texturally too

¹ Contributions from the Phanerogamic Laboratories of Harvard University, no. 32.

² HILL, T. G., Histology of sieve tubes of the angiosperms. *Annals of Botany* 22:265. 1908.

irregular to be used for making radial sections. Phloem from large branches did not show much callus, specimens usually presenting in radial section but two or three rows of sieve tubes with callus.

The material used was cubes about a centimeter each way, which included the cambium as well as the phloem. These were killed, fixed, and softened, and then imbedded in celloidin. For general study the sections were double stained with hematoxylin-safranin and mounted in balsam. Russow's callus reagent was used to demonstrate the callus.

It will be appropriate to consider first the figures which accompany this paper. Figs. 1 and 2 show the topography of the phloem of *Carya alba* under lower power. The sections used for these were stained with hematoxylin-safranin. Fig. 3 is a higher-power magnification of a part of fig. 2. Figs. 4-6 are views of sections of *Carya glabra* that were recently treated with Russow's callus reagent.

Fig. 1 is a radial longitudinal section. At the left side of this section are seen two rows of sieve tubes with portions of end walls showing sieve plates in face view, and along the right side lateral sieve plates are shown in cross-section. The long, narrow, thick-walled cells are bast fibers. These usually occur in groups of three to six as seen in radial view.

The larger phloem parenchyma cells contain prismatic crystals which have elongated, nucleus-like spots in the center. The rays are made up of short parenchyma cells that have several simple pits where they come in contact with phloem parenchyma. A portion of a ray is shown in the left side of this section. No crystals have been observed in the ray parenchyma cells of any of the Juglandaceae studied.

Fig. 2 is a tangential section. Many crystal-bearing phloem parenchyma cells are seen in this view also. The large cells with oblique end walls are sieve tubes. They show the lateral sieve plates very strikingly in face view, and cross-sections of terminal sieve plates on the slanting end walls. This section shows but few bast fibers. The phloem parenchyma cells toward the lower right side of this figure, wherever their starch content is not too dark, may be seen to have densely pitted radial walls. The rays vary from uniseriate to multiseriate.

Fig. 3 is a high-power view of a part of that shown in fig. 2. On the left side there is again a good view of crystal-bearing phloem parenchyma cells. In the center there is a large sieve tube with lateral sieve plates covering the entire tangential wall. These lateral sieve plates when appropriately stained are found to be filled with angular pits with a fine netlike mesh between. They appear to be exactly the same as the terminal sieve plates.

Fig. 4 is a radial section of *Carya glabra*, stained with Russow's callus reagent. At the top and bottom are shown in face view terminal sieve plates covered with callus. Between these two sieve tubes are the dark spots of callus on the lateral sieve plates in cross-section.

Fig. 5 is a view similar to fig. 4. On the right is a portion of a ray showing the parenchyma cells with patches of dark-stained starch grains. On the left is again seen some phloem parenchyma cells containing large crystals.

Fig. 6 shows the center portion of fig. 5 more highly magnified. The dark dashes along the center are cross-sections of the deeply stained lateral callus. The writer has counted 40-50 of these in a straight line along the side of a large sieve tube.

Carya has relatively larger sieve tubes than *Juglans* or *Pterocarya*. In cross-section they are as much larger than the other elements of the tissue as medium sized vessels of the xylem are larger than the tracheids.

The phloem of *Juglans* and *Pterocarya* is much like that of *Carya*, but there are a few general characteristics by which they may be readily separated. The crystal-bearing phloem parenchyma cells of *Juglans cinerea* and *Juglans nigra* are nearly cubical, and each contains a druse, while those of *Carya* are longer than wide and contain prismatic crystals. *Juglans nigra* has very many crystals, especially in specimens from the trunk of large trees. Besides the crystals in the parenchyma, the bast fibers are often filled with rows of cubical crystals. These bast fibers of *Juglans nigra* occur in widely interrupted rings, while in *Juglans cinerea* the rings of bast fibers are nearly continuous. The bast fibers of *Juglans* and *Pterocarya* are thick-walled and keep a more or less circular outline; while *Carya* has relatively much more numerous

elements of the hard bast, yet as these are thinner-walled they tend to collapse and show an irregular outline in cross-sections.

The expanded ends of the large rays of *Juglans cinerea* are noticeable in rather thin specimens of phloem from young trees or small branches, but are seen in only rather thick phloem of *Juglans nigra*. The large sieve tubes of *Juglans nigra* and *Juglans cinerea* have long, crowded, lateral sieve plates like those shown in fig. 3 for *Carya*, but the smaller sieve tubes have sieve plates that are farther apart and have an oval or circular outline.

There are no crystals in the phloem of *Pterocarya* except druses in the parenchyma of root phloem. The phloem of *Pterocarya* has nearly continuous bands of bast fibers alternating with wider bands of sieve tubes and bast parenchyma. The lateral sieve plates in *Pterocarya* are practically the same as in *Juglans*, except that in the larger sieve tubes some of the longer sieve plates are divided obliquely by thin bars. The lateral sieve plates of *Juglans* and *Pterocarya* show equally as well developed callus as *Carya glabra*, though the sieve tubes do not appear to function as long. In some specimens taken from branches of *Pterocarya* and *Juglans*, callus was evident only on the fifth or sixth row of sieve tubes from the cambium. While in similar specimens of *Carya*, callus was present farther from the cambium and was on several rows of sieve tubes.

Where sieve plates occur on the side of a sieve tube next the companion cell, unilateral callus was observed. This callus resembles the unilateral callus described by STRASBURGER³ on the sieve plates of sieve tubes of Abietineae next to the marginal ray cells.

Lateral callus is plentiful in the sieve tubes of *Castanea*, *Salix fragilis*, and *Populus trichocarpa*, though usually not so thick as on the end walls.

A sort of tyloses occurs occasionally in the older sieve tubes of the Juglandaceae. It is formed not by the wall of a parenchyma cell pushing in through a pit, as in the vessels of the xylem, but by a portion of the sieve tube wall subtending a parenchyma cell growing bodily into the sieve tube. The tyloses of the sieve tubes

³ STRASBURGER, ED., Histologische Beiträge 3:1891.



1



4



2



5



3



6

consequently resemble those occurring in the resin canals of certain conifers, rather than those found in the vessels of the angiosperms.

Summary

The six species of the Juglandaceae which have been considered possess well developed lateral sieve plates which have the same structure and appearance and seem to function in the same manner as the sieve plates on the end walls. The callus on the lateral sieve plates is identical in character with that on the end walls. The large sieve tubes have lateral sieve plates which are as crowded and as large as the terminal ones. This is contrary to the accepted views in regard to the sieve tubes of the dicotyledons. It would seem that we have here to do with an ancestral character, which indicates that the lower dicotyledons, as exemplified in the Juglandaceae, are more nearly related to the gymnosperms or vascular cryptogams. It is hoped that a further study of the phloem of the dictoyledons may disclose other ancestral traits, or aid somewhat in a systematic classification from an anatomical standpoint.

This work has been done in the Phanerogamic Laboratories of Harvard University under the direction of Professor E. C. JEFFREY, to whom the writer wishes to express his thanks for assistance and helpful advice.

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EXPLANATION OF PLATE XIII

FIG. 1.—*Carya alba*: radial longitudinal section of phloem. $\times 40$.

FIG. 2.—The same: tangential section of phloem. $\times 40$.

FIG. 3.—A higher-power view of part of what is shown in fig. 2. $\times 180$.

FIG. 4.—*Carya glabra*: radial section stained to show callus on the sieve plates of the sieve tubes. $\times 180$.

FIG. 5.—The same: a similar view of the radial section. $\times 180$.

FIG. 6.—The same: showing a central portion of fig. 5 more highly magnified. $\times 500$.

OENOTHERA LAMARCKIANA: ITS EARLY CULTIVATION AND DESCRIPTION

E. J. HILL

The question raised by Dr. R. R. GATES in a recent number of *Science* (N.S. 31:425. 1910) as to the earliest description and origin of *Oenothera Lamarckiana* Seringe, the importance of which is expressed in a notice in the *BOTANICAL GAZETTE* (50:79. 1910), is the occasion of some historical investigation I have made along the same lines. GATES takes as the earliest description one in manuscript in the form of a long marginal note in a copy of C. BAUHIN's *Pinax*, forming one of the Sturtevant collection in the library of the Missouri Botanical Garden. It was apparently written by one JOANNIS SNIPPENDALE, and is considered as written from the living specimens. In the *Pinax* the plant is called *Lysimachia lutea corniculata*.

GATES gives four characteristics to show that the description applies to a plant of *O. Lamarckiana* and not to *O. biennis* L. or to *O. grandiflora* Ait. These are in the main the form of the rosette leaves, the large flowers, the type of hair arising from reddened papillae, and the quadrangular buds. But taking these as the criteria, I fail to see in what respect it is not essentially the same as a lengthy description made by BAUHIN and published in 1623 in the appendix to the *Pinax* (pp. 520, 521). This of necessity is older than any marginal one placed in a copy subsequent to publication, with the additional advantage of a definite date, if applicable to the same species. The *Pinax* is mainly a bibliography of botany, up to the time of its publication notes or brief characterizations being frequently added to the various topics. In the appendix are corrections of errors made in some of the earlier printed parts, an interruption in the printing affording an opportunity for this, and for the addition of other matter. These are mostly descriptions of plants mentioned in the body of the book, or of new forms, all longer than those customarily given. The longest and fullest of these is *Lysimachia lutea corniculata*, mentioned in the previous *Botanical Gazette*, vol. 51]

part of the work (p. 245), where but five lines were devoted to it, here fifty-three, or more than a column of the double-columned quarto. It has every appearance of being based on the living specimens growing in his garden. Near the close of the account he says:

We received the seed of this [plant], under the name of *Lysimachia virginiana*, from Padua in 1619. Being sown in the spring it remained all summer and winter without a stem, but in the following year produced a stem towards the end of spring and began to flower in June. From the seed, which falls in autumn (for the plant is annual), it blooms abundantly in my garden every year, even up to the close of autumn.

The phraseology on p. 245 is slightly different, and is the one I usually see quoted. Under *Lysimachia lutea corniculata* it is stated:

The seed itself, which was sent from Padua in 1619, grew finely in the garden, and it is readily spontaneous from the fallen seed up to this time.

The account in the appendix may not be in all copies. A second edition of the *Pinax* was published, in references to which I find different dates attached (1661, 1675). On a flyleaf of my copy is written by some unknown hand "Une 2^{me} Edition sans changement parût en 1671." It was a reprint. Authors sometimes cite one of these references, sometimes both, but that on page 245 when but one is given. Thus GRONOVIVS in CLAYTON'S *Flora virginica* (p. 58, 1762), under *Lysimachia lutea corniculata*, gives only p. 245. LINNAEUS, in his *Hortus Cliffortianus* (p. 144, 1737), gives both, but has p. 516 instead of 520, perhaps a typographical error; if not, it shows discrepancies in copies. Much of the description which covers this and other references to *Lysimachia lutea* by various authors cited in RAY'S *Historia plantarum* is a verbatim transcript of BAUHIN'S in the appendix to the *Pinax* (1:862. 1686). There are some omissions and a few minor changes and additions. But these might be needful, as he sought to include variations or forms covered by four descriptive or adjective terms (*virginiana*, *siliquosa*, *corniculata*, and *americana*) published between 1623 (BAUHIN) and 1651 (FABIUS COLUMNA).

The time of introduction of *O. Lamarckiana* into Europe is taken to be about 1614. LINNAEUS (*Hort. Cliff.*) says: "Brought

to Europe 120 years ago [1617 according to date of publication], now become spontaneous and growing everywhere in the sandy fields of Holland." A. DE CANDOLLE (*Géographie Botanique* 2:711. 1855) cites this passage from LINNAEUS, and an additional one from his *Species plantarum* (2d edition): "Hab. in Virginia, unde 1614." This last date is given by LAMARCK and MIRBEL in their *Histoire naturelle des végétaux* (13:82. 1803):

Cette plante originaire de la Virginie et du Canada, a été apportée en Europe en 1614; elle s'y est tellement multipliée qu'on peut la regarder comme naturalisée.

This is of course under the Linnean species *O. biennis*.

But one of the most important passages leading up to the introduction of the plant, and throwing light on its early history, is in the work of DE CANDOLLE just mentioned. He devotes considerable space to the naturalization of plants and the approximate time of introduction into different countries and their most probable place of origin. In his article *Naturalisation à grande distance*, *Oenothera biennis* L. has a prominent place. This includes the different forms segregated by others. After giving the passage quoted above from BAUHIN's *Pinax* (p. 245), but with no allusion to the corresponding one in the appendix or mention of the description there, he says (2:711):

Mon père a vu dans l'herbier de BAUHIN à Bâsle l'échantillon authentique venant d'un jardin, et il a vérifié que c'est bien l'*Oenothera biennis* L. actuellement répandu dans plusieurs parties de l'Europe. L'édition du *Pinax* de 1661 ne dit rien de plus que la première. JEAN BAUHIN n'en parle pas. P. ALPINUS (*Exot. ann.* 1627, p. 325) donne une figure où l'on reconnaît l'espèce; il la nomme *Hyoscyamus virginianus*, et il dit: "Ab hinc annos duos mihi nata est planta ex seminibus nomine *Lysimachiae virginianae* ad me missis a JOANNE MORO medico et philosopho anglo erudissimo." Peut-être cette phrase a-t-elle été écrite quelques années avant la publication de l'ouvrage, par exemple vers 1621 ou 1622, de sorte que la culture dans le jardin de Padoue, dont parle PROSPER ALPINUS, serait la même dont C. BAUHIN faisait mention. Quoi qu'il en soit, il me paraît évident que l'*Oenothera biennis* était alors cultivé dans le jardin de Padoue, comme une plante rare.

The attempt to reconcile dates made in this passage by DE CANDOLLE is readily obviated. He does not seem to recall that ALPINUS died in 1617, and that the work from which he quotes was a post-

humous publication by his son (*De plantis exoticis libri duo*. Venice. 1627), so that he could not have written this in 1621 or 1622, nor sent seeds to BAUHIN in 1619. Born near Venice, ALPINUS became professor of botany in the University of Padua in 1593, and, if not then, somewhere between that time and 1617, the date of his death,¹ became director (*praefectus*) of the botanic garden at Padua.

Though BAUHIN could not have obtained the seed from ALPINUS in 1619, we are not devoid of a clue to the garden at Padua. Fortunately, among other sources for his *Pinax* which BAUHIN gives, is a preliminary page with the heading *Nomina eorum qui plantas vel semina communicarunt*. Three of these were connected with the garden at Padua. The dates are not given, but the order of succession places them: (1) "JACOBUS ANTONIUS CORTUSUS, quintus Patavini horti praefectus"; (2) "PROSPER ALPINUS, Profess. et horti Patavini sextus praefectus"; (3) "JOAN. PREVORTIUS, Med. Professor et horti Patavini septimus praefectus." The succession being without a break, and the time being so short between the death of ALPINUS and the reception of the seed by BAUHIN in 1619, taken in connection with his full and careful record of sources, leaves little room for doubt that they were obtained from PREVORTIUS, the seventh director of the garden.

There is, however, a very narrow interval between the commonly accepted date of introduction from America and the death of ALPINUS (1617), in which he states that he raised plants from seeds obtained from Dr. MORE. For the "two years ago" ("ob hinc duos annos") refers evidently to the time when the plants came up and not to the date of reception. Two years had elapsed between the appearance of the plants and the writing of the account. It would be necessary to place the date of introduction as early as 1614 at least. The figure of the plant in the work of ALPINUS, therefore, must be a representation of one almost at the beginning of its appearance in Europe. DE CANDOLLE, comparing the figures of *Lysimachia lutea siliquosa virginiana* given by PARKINSON in his earliest work (*Paradisus*, 1629) and in his second work (*Theat-*

¹ BAILLON, Dict. de Botanique. Art. PROSPERO ALPINI; SPRENGEL, Gesch. der Bot. 1:356. 1817.

rum, 1640) with that in ALPINUS (*Exot.*, 1627), says that the petals differ, being strongly mucronate in the *Theatrum*, lightly so in the *Paradisus*, emarginate as in the modern plant in ALPINUS, and that PARKINSON'S plant is perhaps different (p. 712). I have seen that in the *Paradisus* (the reprint, London, 1904) and can confirm the statement as to this. The mucro is so broad and low in some of the petals as to give the tips a wavy appearance. The plant is a little branched, and it is stated that it may reach the height of a man. BAUHIN gives this height also. With regard to the form of the petals, DE VRIES mentions a similar discrepancy between the description by LAMARCK of *O. longiflora* Jacq., and the specimen from LAMARCK found in the herbarium of the Museum d'histoire naturelle at Paris. The description says they were rounded, the example shows that they were obcordate.² All tends to show that differences, specific or not, existed in the cultivated plants at so early date that they must have been present in a wild state in America before the introduction into the gardens of Europe.

By whatever means the plants may have reached Europe, we may conclude that the line of transmission of what is now recognized as *O. Lamarckiana* up to the time of the publication of BAUHIN'S description in 1623 was as follows: from JOANNES MORUS of England to PROSPER ALPINUS at Padua, 1614 or earlier; from JOANNES PREVORTIUS of Padua to C. BAUHIN at Bâsle, 1619. His description may therefore be pretty safely dated within nine years or less of the probable introduction.

CHICAGO

² DE VRIES, HUGO, *Die Mutationstheorie* 1:316, 317. 1901.

BRIEFER ARTICLES

MELCHIOR TREUB

(WITH PORTRAIT)

Dr. MELCHIOR TREUB was born at Voorschoten, near Leiden, December 26, 1851, and died at Saint Raphael, near Cannes, October 3, 1910. From 1869 to 1880 he was at the University of Leiden, first as a student and then as an instructor. In 1880 he was appointed Director of the Botanic Garden at Buitenzorg, Java, to succeed Dr. SCHEFFER.

It was in this directorship of nearly thirty years that TREUB displayed that power of organization and of administration, coupled with the spirit of research, which so distinguished him. He found the garden a scientific institution, but he discovered that increased opportunities for scientific work could be secured most readily through cooperation with agricultural interests. Upon this basis he secured private gifts in addition to grants from the government, and under his wise management Buitenzorg became the conspicuous center of research related to tropical agriculture, as well as the best equipped tropical station for purely scientific investigation.

The provisions for visiting botanists are exceedingly generous, the whole atmosphere of the institution suggesting that this is its chief purpose. Not only is there an especially well equipped "visitors' laboratory," but reagents and native collectors are freely supplied. As a result of this liberal policy, combined with the wide range of tropical conditions, the list of visiting botanists is very impressive, both in number and standing.

The *Annals* published by the Garden was established by Dr. SCHEF-



FER, but its editorial management came to TREUB with the second volume. This has been the natural medium of publication for the scientific work of the Garden, and its files represent well the nature and importance of this work. TREUB's own contributions were exceedingly varied, not being guided so much by any special phase of botany as by the opportunity presented by the tropics. Hence they are cited in the literature of morphology, of physiology, and of ecology; and all of them are characterized by clear insight and fine presentation.

His resignation in 1909 was compelled by ill health, brought about in connection with the work of enlarging the scope of the Garden by making it a part of a Department of Agriculture in Java. He intended to live in the Riviera and to prosecute his own studies, but he was forced to spend the winter in Egypt, and did not reach Saint Raphael until spring. It was a great gratification to him that he lived to see the publication of the *Festschrift* in his honor, to which about sixty of his scientific colleagues contributed.—J. M. C.

DAVID PEARCE PENHALLOW

(WITH PORTRAIT)

By the death of Professor D. P. PENHALLOW of McGill University, Montreal, at the untimely age of fifty-six, American Botany has lost a pioneer and leader in his particular field. Born at Kittery Point, Maine, he traveled widely, giving his attention at various times to many different activities. One of the founders and for a time the acting president of the Royal Agricultural College, Sapporo, Japan, he manifested after his return from that country an enthusiastic admiration and even love of the Japanese. Domiciled later for over a quarter of a century in the Dominion of Canada, he became, without losing his American affiliations, so much a part of the academic family of McGill University, that he was, for a number of years one of its Governors. It seems probable that the attempt to carry on his scientific work and at the same time to do his share of the numerous administrative duties which fell to his lot in the country of his adoption, was the primary cause of his early decease.

PENHALLOW's earlier work in his chosen science was on the ascent of sap in wood, and this initial inclination seems to have dominated more or less his whole life. After gaining his degree at Amherst, he set out at an early age for Japan, where he rendered valuable services in connection with the awakening of the scientific activities of that remarkable nation. During his stay in Japan, he visited the Aino in the

northern island and was the first person of western origin to live among them. He collected many data and made many photographs illustrative of his observations among these people, which have unfortunately never been published. His sojourn in Japan, however, had one important result, namely that of directing the attention of the young scientist to the extremely interesting arboreal flora of these islands. After his return to the United States, in 1880, he spent several years in special investigations at Cambridge, Mass. When Sir WILLIAM DAWSON of McGill University called upon ASA GRAY to send him a young man qualified to initiate botanical studies, PENHALLOW was the choice. His relations with Sir WILLIAM DAWSON, a distinguished geologist and paleontologist, gave a paleobotanical bent to the scientific investigations of the young botanist. During his earlier years at McGill, he published a number of articles on fossil plants, some of which were in collaboration with Sir WILLIAM DAWSON. Most important among these are his investigations on the gigantic Devonian seaweeds of Gaspé, Canada, and of another problematic vegetation from the Devonian of Kentucky, including remains of what must now probably be regarded as the earliest fernlike seed plants.

PENHALLOW early saw the need of the structural study of fossil plants, and in his later life was among the most prominent American authorities on the organization of extinct conifers. He gave his special attention to this field for nearly 25 years, publishing, in the early nineties, a key to the identification of coniferous woods, based upon their microscopic structure. The principles laid down by GOEPPERT, KRAUS, and other European masters in this field were used for the elucidation of the structure and affinities of American conifers living and extinct. Professor PENHALLOW was among the very first to attempt to interpret the evolutionary sequence of the conifers in terms of their



internal structure, thus providing a very fruitful and much needed control of the results reached along conventional systematic lines, from the consideration of the superficial characters alone. The early memoir of the *Anatomy of the conifers*, published in the *Transactions* of the Royal Society of Canada, appeared in 1907 in enlarged form as a book. Professor PENHALLOW was among the first to point out the remarkably isolated position of the araucarian conifers, which survive at the present day only in the southern hemisphere.

In those differences of opinion and interpretation which always prevail where scientific investigation is actively carried on, Professor PENHALLOW was a fair-minded and generous opponent. Whatever may be the fate of the particular hypotheses which he advocated, time cannot rob him of the credit of having realized the absolute necessity of attacking the Coniferales from the anatomical side, that is from within. His was a busy life, and within its short span he published articles amounting to upward of 200 titles. His industry and admirable personal qualities were fully appreciated by his scientific colleagues in the United States and Canada. For a number of years he was president of the Natural History Society of Montreal, and was likewise an important influence in the Canadian national scientific organization, the Royal Society of Canada. Nor was he overlooked in his native country. The presidency of the Society of Plant Morphology and Physiology, of the American Society of Naturalists, and of the Botanical section of the American Association for the Advancement of Science bestowed upon him made clear the appreciation of his fellows.—E. C. JEFFREY, *Cambridge, Mass.*

CURRENT LITERATURE

BOOK REVIEWS

The botanical system

In a recent published work,¹ TSCHULOK has sought to give a historical account of the development of the conception of the field of biology, principally botany, and of the logical delimitation of its parts. The historical résumé shows that before SCHLEIDEN (1843) botany had been expanding in ever widening circles of interest until it included the beginnings of almost all the present phases of the subject. The reform movement of SCHLEIDEN swept away all divisions excepting morphology and physiology, with taxonomy occupying an insecure position. This precedent has been followed almost universally, as may be seen by reference to the common general textbooks, such as the Bonn textbook. Ecology, plant geography, paleobotany, etc., are now demanding readmittance to the fold upon equal terms.

TSCHULOK enters into an exhaustive criticism of the several modern systems which have been proposed, and finds that none of them rest upon a logical basis. He then proposes a threefold division. From the standpoint of formal logic, botany is divided into biophysics and biotaxis, the former dealing with "real" relations and the latter with "ideal" relations; from the standpoint of instruction, it may be considered as either general or special; and lastly, there are "seven material viewpoints": (1) taxonomy, (2) morphology, (3) physiology, (4) ecology, (5) chorology, (6) chronology, (7) genetics. It is contended that these divisions include the whole field, and that nothing less will do so. An extended critique justifies this partition of the province of botany, and weighs the claims of such other subjects as pathology and economic botany. It is considered that economic botany, for instance, can have no place as an independent discipline, because in method and material it is in no way to be distinguished from these seven divisions, but rather it is part and parcel of each of them.

The consequences of circumscribing the field of botany, as is commonly done in "general" texts, is given full prominence. A single illustration will suffice. For a half-century paleobotany has been out of the texts and out of the usual courses of instruction. It has also been out of the minds of students, and those who might have taken up research in this field have been guided into other sorts of activity merely because of a lack of opportunity for a general outlook over the whole field of botany. As a result, the examination of this very important material has been left almost wholly to geologists who are usually quite untrained in botany.

¹ TSCHULOK, PHIL. S., *Das System der Biologie in Forschung und Lehre*. pp. x + 409. Jena: Gustav Fischer. 1910.

At the present time, when many relatively new branches of botany are demanding recognition as coordinate with the old, such a critique of the historical and logical background of the science is especially welcome.—W. L. EIKENBERRY.

American men of science

President JORDAN's recently issued collection of biographical sketches² brings together in a single volume and in very pleasing form the personal history and prominent achievements of seventeen American scientific leaders. The sketches are in all instances by a friend, a colleague, or at least a *Fachmann* of the scientist treated, and as a result combine in high degree insight and sympathy. The selection of the seventeen scientists most worthy to be included in such a series must have offered some difficulty, though such appropriate names as AGASSIZ, AUDUBON, RUMFORD, GRAY, DANA, and some others will occur at once to the layman as well as to the scientific student. The distribution as to subject is not without interest. Of physicists there are four, and of zoologists three; while ornithology, paleontology, and geology have two each; and botany, chemistry, anatomy, and astronomy claim each a single representative.

The interest of the botanical reader will naturally center upon the account of Dr. GRAY, whose life and work are treated with obvious affection by his pupil and friend Professor JOHN M. COULTER. Sketching clearly what is known of Dr. GRAY's early history, he brings out vividly as he proceeds the unity of purpose, unflagging diligence, extraordinary capacity, and grand achievements which characterized GRAY's career. Finally, he is able from personal acquaintance to add many more intimate touches, which give life to the sketch and make the reader feel acquainted with the charming personality of its subject. As those capable of giving them decrease, these personal reminiscences of Dr. GRAY become the more precious.

In perusing the various biographies here assembled, one is impressed by the fact that GRAY more than any other of these men, if perhaps we except Count RUMFORD who lived in Europe, and AGASSIZ who was born and educated there, stood in the closest relation to European activities in his science and did much to correlate and harmonize the intellectual endeavors of the New World and the Old.

Without any lack of patriotism it may be pointed out to publishers that works on distinguished Americans are rendered no more attractive by much gilt or by a squashed eagle painfully recalling the unhappy bird on the demonezied trade dollar. However, notwithstanding its forbidding appearance, the volume furnishes fascinating reading and gives information and stimulus in no small measure. "There were giants in the earth in those days."—B. L. ROBINSON.

² Leading American men of science. Edited by DAVID STARR JORDAN. Illustrated. 8vo. pp. 471. New York: Henry Holt & Co. Forming one of a series of volumes, edited by W. P. TRENT, devoted to biographies of leading Americans.

NOTES FOR STUDENTS

Graft hybrids and chimeras.—The large amount of recent work on graft hybrids, which has resulted in such astonishing discoveries as to their exact nature, seems to call for a collective review. In 1825 M. ADAM, a French horticulturist, by grafting *Cytisus purpureus* (a small tufted species) on *Laburnum vulgare* (an arborescent species) was much surprised to find that there resulted a shoot with somewhat intermediate characters. While the original individual has long been dead, the new form has been propagated by grafting and is somewhat common in cultivation; to it there has been given the name *Laburnum Adami*, and generally it has been regarded as a graft hybrid. Scarcely second in reputation to this, the most famous of the "graft hybrids," is *Crataegomespilus*, which is supposed to be a graft hybrid between *Crataegus monogyna* and *Mespilus germanica*; in this case the original tree is said still to exist in Lorraine. A third supposed case of a graft hybrid is the Bizzaria orange, which is thought to have arisen through the intergrafting of *Citrus Aurantium* and *C. medica*. While much study has been made of these peculiar plant forms, it is only very recently that their nature has been understood.

The present phase of graft hybrid investigation dates from a paper by HANS WINKLER, published in 1907.³ Although the results of this first paper were somewhat disappointing, they deserve mention, because they opened up a new method of investigation. A scion of *Solanum nigrum* was grafted on *S. Lycopersicum*, and after growth had been resumed, a transverse cut was made in such a way as to sever both stock and scion, it being hoped that adventive shoots would grow from the cut surface along the line of contact of stock and scion. Such adventive shoots actually appeared, and in one case the new shoot involved tissues of both stock and scion. However, the new form was not a graft hybrid, for clearly one side of the shoot was *Solanum nigrum* and the other *S. Lycopersicum*; to this peculiar structure WINKLER gave the suggestive name *chimera*. So sharply marked was the line between the tomato and the nightshade that some leaves were partly of one species and partly of the other. WINKLER's method soon yielded the results he had been seeking, for in 1908 he announced the production of a true graft hybrid,⁴ a notable result, since never before had this been done under exact experimental control. To the new form there was given the name *Solanum tubingense*, in honor of the university town where the plant was produced. Out of 268 grafts between the tomato and the nightshade, there arose over 3000 adventitious shoots, among which there were five chimeras and the supposed graft hybrid *Solanum tubingense*; the latter, while intermediate in character, is somewhat closer to the nightshade than to the tomato. Early in 1909 WINKLER reported

³ WINKLER, HANS, Ueber Propfbastarde und pflanzliche Chimären. Ber. Deutsch. Bot. Gesell. 25:568-576. figs. 3. 1907; see BOT. GAZETTE 47:84. 1909.

⁴ ———, *Solanum tubingense*, ein echter Propfbastard zwischen Tomate und Nachtschatten. Ber. Deutsch. Bot. Gesell. 26a:595-608. figs. 2. 1908; see BOT. GAZETTE 47:250. 1909.

the production of several more "graft hybrids" by the use of the same methods.⁵ In this paper four varieties of graft hybrids are described, and are given the names *Solanum Darwinianum*, *S. Gaertnerianum*, *S. proteus*, and *S. Koelreuterianum*; the first two resemble the nightshade more than the tomato, while the last two are closer to the tomato. Some of the new forms appeared more than once in the cultures, *S. Gaertnerianum*, for example, being observed to arise five times. Some of the new forms appeared as branches from chimeras. In a recent paper⁶ WINKLER reports the results of a study of the progeny of the new forms. Although the vegetative shoots seem able to fuse and merge readily in various ways, the tomato and nightshade cannot be hybridized sexually. WINKLER observes that the "graft hybrids" without exception revert to the nearer parent, the seedlings of *Solanum tubingense*, *S. Darwinianum*, and *S. Gaertnerianum* always being *S. nigrum*, while the seedlings of *S. proteus* and *S. Koelreuterianum* always are *S. Lycopersicum*. The new forms may be hybridized sexually with the nearest parent form, the progeny being pure nightshade or tomato, as the case may be. Furthermore, reversion in the vegetative shoots is to the nearer parent form.

While WINKLER's results are accepted without debate, his interpretation has been called in question by various investigators. It may be noted that the behavior of the new *Solanum* forms is altogether like that of *Laburnum Adami*, which often shows vegetative reversion to one of the parent forms, and whose seeds give rise not to *L. Adami*, but to *L. vulgare*. STRASBURGER, who always has consistently opposed the reality of graft hybrids on cytological grounds, has taken up the new *Solanum* forms, calling them *hyperchimeras*, that is, more or less complicated chimeras, in which the elements of the two parent forms are more or less intermingled but without any real nuclear fusion (see below).⁷ Of much greater significance are some recent investigations by ERWIN BAUR, and his results bid fair not only to cause a different interpretation to be placed upon WINKLER's results than has been made by either WINKLER or STRASBURGER, but to revolutionize our notions along certain lines as to the possibilities of plants. BAUR has found from a careful study of geraniums with white-margined leaves⁸ that the green cells and colorless cells each are descended from others of their kind, the peripheral portions (composing two or three rows) being colorless (though containing chromatophores) and the internal portions green, and the limits between them being

⁵ WINKLER, HANS, Weitere Mitteilungen über Propfbastarde. Zeitschr. Bot. 1:315-345. pl. 1. figs. 4. 1909; see BOT. GAZETTE 48:478. 1909.

⁶ ———, Ueber die Nachkommenschaft der *Solanum*-Propfbastarde und die Chromosomenzahlen ihrer Keimzellen. Zeitschr. Bot. 2:1-38. 1910; see BOT. GAZETTE 49:386. 1910.

⁷ STRASBURGER, EDUARD, Meine Stellungnahme zur Frage der Propfbastarde. Ber. Deutsch. Bot. Gesell. 27:511-528. 1909.

⁸ BAUR, ERWIN, Das Wesen und die Erblchkeitsverhältnisse der "Varietates albomarginatae Hort." von *Pelargonium zonale*. Zeit. Abst. Vererbungslehre 1:330-351. figs. 20. 1909; see BOT. GAZETTE 48:72. 1909.

sharp. Since the sexual cells are from the peripheral white portion, the seedlings give pure white forms. White branches give only white forms vegetatively, and green branches only green forms. If a pure white and a pure green form are hybridized sexually, there result, besides pure white and pure green offspring, green-white mosaics. If in the latter the growing point is situated on the line between the white and green portions, there results a chimera, such as WINKLER obtained so frequently in *Solanum*. Since in a cross-section of a stem the two components appear as sectors, BAUR has given to such forms the name *sectorial chimeras*. For the condition that BAUR finds in an ordinary *Pelargonium* with white-margined leaves, he gives the name *periclinal chimeras*, one of the components investing the other; in *Pelargonium* the growing point is periclinally divided into white and green cells, the former outermost, so that the entire plant is composed of a body of green geranium invested by a mantle, two or three cells deep, of white geranium. In referring to WINKLER'S work, BAUR suggested that the so-called graft hybrids of *Solanum* probably are periclinal chimeras. In another paper⁹ he discusses STRASBURGER'S theories concerning hyperchimeras, noting that such an irregular mixture of the elements of the two component forms can hardly give rise to such definite structures as the so-called graft hybrids. Very recently BAUR has published a résumé of his work on *Pelargonium*, and on the graft hybrid question generally.¹⁰ He has discovered also that *Crataegomespilus* is a periclinal chimera, the form known as *C. Asnieresii* being composed of a *Crataegus* body with a *Mespilus* epidermis; while the form known as *C. Dardari* has a *Mespilus* periphery of two cell layers. *Laburnum Adami*, which has been a riddle for nearly a century, proves to be a periclinal chimera, with an epidermis of *Cytisus purpureus* and a body of *Laburnum vulgare*; seedlings are always the latter, because the hypodermal layer, which gives rise to the sex cells, is of that species. When the peripheral species is composed of two or more layers, the seedlings are of that species, as in *Pelargonium*. One of the most interesting features of a situation that is throughout of absorbing interest is that BAUR'S remarkable discovery was almost made by MACFARLANE¹¹ fifteen years ago, as BAUR himself points out. MACFARLANE made a careful anatomical study of *Laburnum Adami* in comparison with *Cytisus purpureus* and *Laburnum vulgare*, and an examination of his figures shows clearly that *Laburnum Adami* agrees with *Cytisus purpureus* as to its epidermis, and with *Laburnum vulgare* as to its body. Indeed MACFARLANE says: "The very striking resemblance which the epidermis of the hybrid portion has to that of *C. purpureus* . . . would seem at first sight to prove that

⁹ BAUR, ERWIN, Propfbastarde, Periklinalchimären, und Hyperchimären. Ber. Deutsch. Bot. Gesell. 27:603-605. 1910.

¹⁰ ———, Propfbastarde. Biol. Centralbl. 30:497-514. figs. 7. 1910.

¹¹ MACFARLANE, J. M., A comparison of the minute structure of plant hybrids with that of their parents, and its bearing on biological problems. Trans. Roy. Soc. Edinburgh 37:203-286. 1895.

the hybrid portion was wrapped around, so to speak, by an epidermis of *C. purpureus*." Very recently BUDER has reinvestigated *Laburnum Adami*,¹² and has brought additional evidence to show that BAUR's view is correct. Finally, WINKLER, in his latest paper,¹³ states that a study of his *Solanum* forms from BAUR's viewpoint discloses that for the most part they are, as BAUR thought likely, periclinal chimeras. Here he suggests that what have been taken to be graft hybrids may (theoretically) be actual graft hybrids, resulting from the fusion of the somatic cells of different species; or again they may have a hybrid nature, owing to the migration between stock and scion of various substances (as atropin or nicotin in the Solanaceae); or finally they may be chimeras, where the possibility lies open that they may be hyperchimeras, sectorial chimeras, or periclinal chimeras. Careful cytological study has shown that *Solanum tubingense*, *S. proteus*, *S. Koelreuterianum*, and *S. Gaertnerianum* are periclinal chimeras. *S. tubingense* has a nightshade body and a tomato epidermis; *S. Koelreuterianum* has the reverse relation of the two components; *S. proteus* has a tomato periphery of two cell layers, and it is probable that *S. Gaertnerianum* has the reverse relation. WINKLER thinks, however, and the cytological evidence noted is confirmatory, that in *Solanum Darwinianum* he has a true graft hybrid that was produced by the fusion of vegetative cells of the nightshade and tomato. If this is proven to be correct, it will stand, not only as the first experimentally produced graft hybrid, but as the only certain instance on record of such a form. The discoveries of WINKLER and BAUR open a new path in experimental biology, and to one as much as to the other belongs the credit that goes to the pioneer; to WINKLER, because his brilliant work has made possible the experimental study of these problems, and because his studies mark the opening of a new line of investigation; to BAUR, because he has solved the riddle of nearly a century, and because he has made possible the interpretation of WINKLER's results. It goes without saying that biologists will wait with eager expectancy the announcement of new results, and that many experimenters will be attracted to the new field.—HENRY C. COWLES.

The cytological aspect of graft hybrids and chimeras may be summarized as follows:

In 1905 and 1907, in papers dealing with the rôle of the chromosome in heredity, STRASBURGER¹⁴ included an account of his investigations upon

¹² BUDER, JOHANNES, Studien an *Laburnum Adami*. Ber. Deutsch. Bot. Gesell. 28:188-192. 1910.

¹³ WINKLER, HANS, Ueber das Wesen der Propfbastarde. Ber. Deutsch. Bot. Gesell. 28:116-118. 1910.

¹⁴ STRASBURGER, E., Histologische Beiträge zur Vererbungsfrage. I. Typische und allotypische Kernteilung. Jahrb. Wiss. Bot. 42:1-70. pl. 1. 1905.

———, Ueber die Individualität der Chromosomen und die Propfhybriden-Frage. Op. cit. 44:482-555. pls. 5-8. 1907.

Laburnum Adami. If this plant is really a hybrid, owing its origin to a fusion of diploid nuclei of *Laburnum vulgare* and *Cytisus purpureus*, its nuclei should be tetraploid; but they were found to be only diploid, and STRASBURGER regarded this as evidence against the hybrid character of the graft. After NĚMEC¹⁵ had reported vegetative fusions of nuclei followed by reduction phenomena in chloralized root tips, STRASBURGER repeated the experiments, but could not confirm NĚMEC's results, and therefore concluded that they had no significance so far as *Laburnum Adami* was concerned, and also that in the structure of their nuclei, plants known as graft hybrids show no indication of a hybrid character.

At this stage in the development of the subject, WINKLER¹⁶ secured from *Solanum Lycopersicum* and *S. nigrum* plants which were acknowledged to be graft hybrids, and he asserted that they would necessitate a fundamental revision of our theories in regard to inheritance, and especially in regard to the rôle of the nucleus in heredity. Since the threatened theories were due to STRASBURGER more than to any other botanist, he felt called upon to defend them, and securing material by grafting *Solanum Lycopersicum* and *S. nigrum*, he examined the nuclei, but did not find them to be different from those of other graft hybrids which he had previously investigated. There was no migration of nuclei, no fusion of nuclei of scion and stock, or any regulative reduction processes. He would regard WINKLER's graft hybrids as more or less complicated chimeras and would call them "hyperchimeras."

In many angiosperm parasites (like mistletoe) the relation between parasite and host is very intimate, but there is no mingling of nuclei. In grafting, it seems possible that a bud from the point of union might give rise to a shoot bearing a flower in which an anther might be from the scion and an ovary might be from the stock. Close fertilization might then give rise to a true hybrid, but hyperchimeras, STRASBURGER thinks, would be more likely to produce flowers, the seeds of which would give rise to pure plants of either the scion or stock.

The fact that pollen from his graft hybrids would cause fertilization in *Solanum nigrum* or *S. Lycopersicum*, while neither of these plants can be crossed with the other, WINKLER regards as proof of hybrid character; but STRASBURGER thinks that the pollen was probable pure, and consequently fertilization was to have been expected, but that only *S. nigrum* or *S. Lycopersicum* would result.

STRASBURGER publishes no figures and refrains from giving a detailed account of nuclear phenomena, because WINKLER's full paper has not yet been published; but his examination satisfies him that WINKLER has produced

¹⁵ NĚMEC, B., Ueber die Entwicklung des Chloralhydrats auf die Kern- und Zellteilung. Jahrb. Wiss. Bot. 39:645-730. 1904.

¹⁶ WINKLER, HANS, Weitere Untersuchungen über Propfbastarde. Zeitschr. Bot. 1:315-345. pl. 1. figs. 4. 1909.

nothing which demands any fundamental revision of his theories in regard to the rôle of the nucleus in heredity.

Soon after this paper by STRASBURGER appeared, WINKLER¹⁷ published a description of the generation obtained from the seed of his graft hybrids, and includes an account of the chromosome numbers. In *Solanum Lycopersicum* the x and $2x$ numbers are 12 and 24; while in *S. nigrum* they are 36 and (probably) 72. He suggests that the difference in chromosome numbers may prevent the crossing of these two species, although he recalls that ROSENBERG crossed two species of *Drosera* with 10 and 20 chromosomes in their x generation, and obtained a hybrid with 30 chromosomes as the $2x$ number. If the *Solanum* graft hybrids are due to a fusion of somatic nuclei, they should have $72+24$, or 96 chromosomes, unless the fusion should be followed by a regulative reduction, in which case the number should be 48. WINKLER found the x number to be 36 in *Solanum tubingense*, *S. Darwinianum*, and *S. Gaertnerianum*, and found 12 in *S. proteus* and in *S. Koelreuterianum*, the first three of these, in their pollen formation, reverting to *S. nigrum*, and the other two reverting to *S. Lycopersicum*. The sterility of *S. Koelreuterianum* and *S. Darwinianum* might be due to a difference in chromosome numbers of microspores and megaspores. The microspore number is 12, but the megaspore number remains to be determined. In all five of the graft hybrids the development of the pollen is regular, but it is still to be determined whether the germ cells are pure or hybrid. WINKLER thinks it is more reasonable to suppose that the graft hybrids more closely resembling *S. nigrum* are from *S. nigrum* cells, and that those resembling *S. Lycopersicum* are from cells of that parent, the nuclei being those of one parent or the other, but the cytoplasm being mingled with that of neighboring cells. If such cytoplasm should have so great an influence, it would interfere with the theory that the nucleus is the sole bearer of hereditary characters.

In an addendum to this paper WINKLER severely criticizes STRASBURGER for publishing anything before the cytological details had been made public. STRASBURGER certainly would not have taken part in the matter had it not been that his cytological theories had been attacked. Had some cytological evidence accompanied WINKLER's attack upon theories which STRASBURGER has held and defended almost for a lifetime, any unpleasantness could have been avoided. In this addendum WINKLER states that in September 1907, at the Dresden meeting of the *Deutsche botanische Gesellschaft*, he had suggested that the *Solanum* graft hybrids might be complicated chimeras, a sort of mosaic of the two parents. This suggestion seems to the reviewer to be a good working hypothesis, and if the suggestion is really a fact, an intensive study of the nuclei and cytoplasm of the graft might enable one to recognize, even in vegetative tissues, just what cells have been derived from each parent, while in the reduction divisions the recognition should not be difficult.

¹⁷ WINKLER, HANS, Ueber die Nachkommenschaft der *Solanum*-Propfbastarde und die Chromosomenzahlen ihrer Keimzellen. *Zeitschr. Bot.* 2:1-38. 1909.

That there is an interchange of material between nucleus and cytoplasm probably all cytologists will admit, although optical evidence is at present very scanty. It seems quite possible that the whole graft hybrid and chimera question, when the cytological evidence is all in, will emphasize rather than weaken the theory that the nucleus is practically the sole bearer of hereditary characters.

In his most recent account of the chromosomes of these forms WINKLER¹⁸ finds that *Solanum tubingense*, *S. proteus*, *S. Koelreuterianum*, and *S. Gaertnerianum* are periclinal hybrids; while *S. Darwinianum*, at least in the subepidermal layer of the stem apex, is a fusion hybrid (*Verschmelzungs-Propfbastard*). The germ cells of this latter form have 48 chromosomes, and since the parents (*S. nigrum* and *S. Lycopersicum*) have 12 and 36 chromosomes as the reduced numbers, WINKLER infers that the subepidermal layer from which the pollen is derived must have 48 chromosomes; and he supposes that a *S. nigrum* cell with 24 chromosomes has fused with a *S. Lycopersicum* cell with 72, giving rise to a nucleus with 96; and that in the progeny of this nucleus the number has become reduced to 48. Another reduction would then give the required 24. This seems too complicated to be correct.

It is evident that cytological investigation of graft hybrids has only just begun. STRASBURGER early recognized the importance of such investigation, and WINKLER's splendid success in securing the grafts has reopened an attractive field for cytological research. The problems are so numerous and the time demanded for reliable results is so great that one man cannot hope to do all the work. Many have tried to find out whether there is a cytological basis for Mendelism. DEVRIES has welcomed cytological investigations of mutation and has generously furnished material for such work. If WINKLER should welcome others into the field, the facts might soon be uncovered; but if others must wait until he has finished, the task is so great and so complicated that, although a young man, he might grow old with the problem still unsolved. —CHARLES J. CHAMBERLAIN.

Plant diseases.—*Cyanospora albicedrae*, a new generic type, is reported on the mountain cedar of Texas by HEALD and WOLF.¹⁹ The fungus is a pyrenomycete of a peculiar type, having its perithecia prostrate, with the short ostecolium curved outward. The perithecia occur singly or in small groups on whitened areas on the trunks and branches. This whitening of the bark is the most characteristic symptom of the infected trees. The fungus is supposed to be a parasite, although its parasitism is not certain. The present paper is limited to a description of the fungus and its effect on the trees.

A new *Macrophoma* (*M. Phoradendri*) on *Phoradendron flavescens* (Pursh)

¹⁸ WINKLER, HANS, Ueber das Wesen der Propfbastarde. (Vorläufige Mitteilung.) Ber. Deutsch. Bot. Gesell. 28:116-118. 1910.

¹⁹ HEALD, F. D., and WOLF, F. A., The whitening of the mountain cedar, *Sabina sabinoidea* (H. B. K.) Small. Mycologia 2:205-212. pl. 31. figs. 3. 1910.

Nutt. is described by WOLF²⁰ in the same journal. It infects the leaves, which it causes to fall.

An interesting organism belonging to the small group of parasitic slime molds (Phytophycaceae) is described by SCHWARTZ²¹ as occurring on the roots of some species of the Juncaceae. The organism belongs in the genus *Sorosphaera*, and in its development closely resembles the classic example of this group, *Plasmodiophora Brassicae* Woronin. In the earliest stages observed, the parasite consists of small multinucleate amoebae in the root hairs and outer cortical cells of the infected plants. The roots show no hypertrophy, and scarcely any other outward sign of the presence of the parasite, which can be discovered only by microscopic examination. In the vegetative stage all the nuclei of the amoebae divide simultaneously by the formation of a chromatic ring or plate surrounding an elongated karyosome. The process is identical with that described for *Plasmodiophora Brassicae*. At the beginning of spore-formation the protoplasm of the amoebae separates into a number of amoebulae, each with a single nucleus. The nuclei of the amoebulae undergo two divisions, forming four uninucleate spores. The spores remain loosely aggregated in sorospheres; their germination was not observed. The paper concludes with a brief description of *Entorrhiza cypericola*, a member of the Ustilagineae inhabiting the roots of various species of *Juncus*.

BROOKS gives an account²² of the development of *Gnomonia erythrostoma*, which causes the leaf-scorch disease of the sweet cherry. The mycelium, which is intercellular in the tissues of the leaves, consists of multinucleate cells, resembling in this respect other ascomycetes except the mildews. The first fruiting organs to appear are spermagonia, which are produced in great numbers on the lower surface of the leaves. The spermatia, which are discharged from the spermagonia in enormous numbers, are single-celled filamentous bodies with large nuclei and little cytoplasm. This structure, which BLACKMAN has pointed out as characteristic of male cells, leads the author to regard the spermatia as abortive male cells. The perithecia originate, as in other ascomycetes, as interwoven masses of hyphae near the lower epidermis. Branches from some of the outer cells of the mass protrude through the stomata of the leaf and bear a superficial resemblance to trichogynes. No case of their functioning as such was observed, however, although it often happens that a number of spermatia become attached to the protruding hyphae, a fact easily explicable when one considers the enormous number of spermatia produced. That the projecting hyphae do not function as trichogynes is further

²⁰ WOLF, F. A., A leaf blight on the American mistletoe, *Phoradendron flavescens* (Pursh) Nutt. *Mycologia* 2:241-244. *pl.* 32. 1910.

²¹ SCHWARTZ, E. J., Parasitic root diseases of the Juncaceae. *Annals of Botany* 24:511-522. *pl.* 40. 1910.

²² BROOKS, F. T., The development of *Gnomonia erythrostoma* Pers., the cherry leaf-scorch disease. *Annals of Botany* 24:585-605. *pls.* 48, 49. 1910.

shown by the fact that they sometimes occur apart from any connection with the young ascocarps. Moreover, the development of asci proceeds in a region remote from the "trichogynes." The ascogonial hyphae are differentiated in the basal part of the mass of interwoven hyphae; they are characterized by their larger size and larger nuclei. No nuclear fusions were observed in the ascogonia, which seem to have lost their function and appear soon to degenerate. Apparently the ascogenous hyphae do not arise from them, but from other hyphae near the base of the perithecium, which appear after the ascogonia disintegrate. The asci arise from the terminal part of the ascogenous hyphae without the hook-formation common in ascomycetes. Other cells of the ascogenous hyphae may also grow out into asci. The ascus cells contain two nuclei which fuse as usual, whereupon three successive divisions occur, forming the eight spore-nuclei. The first of the three divisions is regarded as a reduction division, to counterbalance the single fusion which was observed. After the spore membrane has been formed, the nucleus of each spore divides again, a septum dividing the spore into two unequal cells being formed between the daughter nuclei.—H. HASSELBRING.

Insect galls.—The past few years have demonstrated an increasing interest in the study of cecidology, and, as in all biological subjects, the first work is taxonomic. A few of the interesting papers of the past few months are as follows: PEREZ²³ discusses the cecidia of *Eritrea*, describing 36 species of galls and one gall-maker. The descriptions are clear and the technical names of the host plants are given, but there are no figures. The VAN LEEUWEN-REIJNVAANS²⁴ discuss the cecidia of Java, describing 150 species on almost as many host plants. Most of these galls were collected at Salatiga at an elevation of about 600 meters; and they were found to be much more abundant in the moist than in the dry localities. Descriptions are given of the galls, and in many cases of the insects also, but the authors state that in describing the gall it is not necessary to describe the gall-maker, a view which is contrary to the views of some of our American entomologists, but with which the reviewer is in hearty sympathy. Most of the descriptions are accompanied by good figures. TROTTER²⁵ gives descriptions of 19 species of galls occurring on 14 host plants. His descriptions also include the bibliographies of those previously described. HOWARD²⁶ has described 52 species of Dr. SICHEL'S collection, which is deposited in the Entomological Museum of Natural History in Paris. He also mentions a number of old galls of unknown origin. MASSALONGO²⁷

²³ PEREZ, T. DE STEFANI, Altri Zoocecidii dell' *Eritrea*. Marcellia 8:7-18. 1909.

²⁴ LEEUWEN-REIJNVAAN, J. und W., DOCTORS, Einige Gallen aus Java. *Op. cit.* 8:21-35, 85-122. 1909; 9:37-61. 1910.

²⁵ TROTTER, A. Nuovi Zoocecidii della Flora Italiana. *Op. cit.* 8:50-59. 1909.

²⁶ HOWARD, C., Les collections cécidologiques du Laboratoire d'Entomologie du Museum d'Histoire Naturelle de Paris: L'Herbier du Dr. SICHEL. *Op. cit.* 65-78.

²⁷ MASSALONGO, C., Galle e simili produzioni anormali. *Op. cit.* 133-141.

gives descriptions, with bibliography and in some cases figures, of 15 species. PANTANELLI²⁸ gives a lengthy description of a mite (*Eriophyes*) of the olive and also a description of its gall. RUBSAAMEN,²⁹ continuing his studies on the European cecidia, describes, and in many cases figures, 42 species, 4 of which are new. BAYER³⁰ in a paper on the cecidia of Bohemia gives a bibliography of 32 titles and lists 198 cecidia.

For a number of years the anatomy or rather the histology of cecidia has proved an interesting field for the European workers, but only in recent years has it attracted the attention of the American students. A recent paper is that of GREVILLIUS³¹ on the anatomy of the thysanopterous cecidia of *Vicia Cracca*. This gall is very conspicuous because of the curling and twisting of the leaves which are infested with the insects, whose eggs can be found between the epidermis and mesophyll. In the more advanced stages the palisade cells lose their characteristic forms and become isodiametric. These galls never develop the complicated structures found in those produced by the hymenopterous insects.

Although the physiological problems connected with the study of insect galls have long been looked upon with interest, the difficulties have been so great that few have had the courage to attack them. One of the recent papers on this subject is by NALEPA,³² who has taken up a study of the gall-inhabiting ants. This subject has been investigated by others, among them PEYRITSCH, who considered light the most important factor because there were more galls on plants growing under shade than in the light. NALEPA'S work took into consideration the relative importance of light, temperature, and moisture, and involved a number of experiments in which the insects were kept in cylinders, in which these factors could be controlled. In this connection he studied also other insects, such as *Eriophyes*, which he found were uninfluenced by the light. His results in general confirm the views of PEYRITSCH.—MEL T. COOK.

Transpiration.—RENNER³³ has published a paper on the physics of transpiration. It adds a number of important facts to the epoch-making work of BROWN and ESCOMBE on multiperforate septa. He works out mathematical formulae for the resistance to the passage of water vapor offered by stomatal apparatus of various xerophytes. The experimental part is carried out with models having the shape of xerophytic transpiratory canals and with plants

²⁸ PANTANELLI, E., Un Eriofide nuovo sull' olivo. *Op. cit.* 142-146.

²⁹ RUBSAAMEN, EU. H., Beiträge zur Kenntnis aussereuropäischer Zoocecidien. *l.c.* 9:3-36. 1910.

³⁰ BAYER, EMILE, Les Zoocécidies de la Bohême. *Op. cit.* 63-104.

³¹ GREVILLIUS, A. Y., Ein Thysanopterocecidium auf *Vicia Cracca* L. *Op. cit.* 8:37-45. 1909.

³² NALEPA, A., Der Heliotropismus der Gallmilben und seine biologische Bedeutung. *Op. cit.* 78-84.

³³ RENNER, O., Beiträge zur Physik der Transpiration. *Flora* 100:451-547. 1910.

themselves. In agreement with BROWN and ESCOMBE, he states that loss of water vapor from leaves is through static diffusion, and that it is proportional to the differences of density of the vapor inside and outside the leaf. RENNER urges, as a thing of great importance, that the rate of diffusion will be inversely modified by an increase in the distance between the region of minimum density outside the leaf and the maximum density within the leaf. It is with methods by which this distance is modified that he is mainly interested. If the distance is great, the gradient is low and the flow is slow; if the distance is small, the gradient is high and the flow fast. One way in which this distance is increased in still air is by the water vapor cap which forms over the surface of the leaf. The larger the leaf, the greater the average thickness of the vapor cap. For this reason, in still air the amount of transpiration does not vary with the surface of the mature leaves, but is proportionally less for the larger leaves. RENNER believes that if the air were absolutely still it would vary as the diameter of the leaves.

Winds increase the transpiration of small mature leaves by a much greater percentage than it does the large ones. In wind the transpiration is proportional to the surface of the leaves. Again, the distance between the internal maximum vapor pressure and the external minimum may be increased by external or by substomatal cuticular cavities; if of the same size and shape, RENNER finds that the two have equal effects.

RENNER devised a means of experimentation by which he located the point of saturation within a rapidly transpiring leaf. He believes it often lies some distance from the stomata. In such cases a considerable system of intercellular spaces is involved in the diffusion. He emphasizes the fact that in such cases the stomata, if open, are only a small part of the diffusion canals, and therefore play a small part in the control of transpiration. In a similar way their importance as controlling factors is modified by internal and external cuticular chambers, and even by the vapor cap.—WILLIAM CROCKER.

Infection experiments with rusts.—In a preliminary report of some infection experiments made near Neuenburg (Switzerland), MÜHLENTHALER³⁴ shows that teleutospores of the *coronata* type of *Puccinia* from *Calamagrostis varia* produced aecidia on *Rhamnus alpina* and *R. Purshiana*. Aecidiospores from these reinfected *Calamagrostis varia* and *C. tenella* among several grasses tried. Aecidiospores collected on *R. cathartica* produced uredospores on *Bromus erectus* var. *condensatus*, *Festuca alpina*, *F. arundinacea*, *F. gigantea*, and *F. varia*. The uredospores thus produced on *Bromus erectus* var. *condensatus* could be transferred to *B. erectus* and its var. *condensatus*, *B. inermis*, *B. sterilis*, and *B. tectorum*.

In continuation of his cultural work on the Uredineae, ARTHUR³⁵ reports

³⁴ MÜHLENTHALER, F., Infektionsversuche mit Kronenrosten. Centralbl. Bakt. II. 26:58. 1910.

³⁵ ARTHUR, J. C., Cultures of the Uredineae in 1909. Mycologia 2:213-240. 1910.

the results of cultures of 1909, marking the beginning of the second decade of the work. In the season covered by the report, 15 species of rusts were each sown on a large number of aecidial hosts with negative results. Sowings of 23 species were made supplementing or confirming previous work of the author and others. Of special interest among these is the sowing of *Calypsotheca columnaris* on potted plants of *Abies Fraseri*. The successful culture of the aecidia on *Abies* led to the subsequent discovery of the native aecidial form on *Abies balsamea* in Nova Scotia, whence the original *Calypsotheca* material had been obtained. This collection of the aecidia by Professor FRASER is the first from America. Of teleutospore forms connected for the first time with aecidial forms, 6 are reported. These are *Puccinia Ceanothi* (Ellis and Kellerm.) Arth. on *Andropogon Hallii* Hack. and *Ceanothus americanus* L.; *Gymnosporangium exiguum* Kern on *Juniperus virginiana* L. and *Crataegus Pringlei* Sarg.; *G. corniculans* Kern on *J. horizontalis* Moench, *Amelanchier erecta*, and *A. canadensis* (L.) Medic.; and *G. trachysorum* Kern on *J. virginiana* L., *Crataegus punctata* Jacq., *C. coccinea* L., and *C. cernis* A. Nels.—H. HASSELBRING.

Rate of photosynthesis.—THODAY³⁶ comes to the defense of the increased weight method of SACHS for determining the rate of carbon fixation in green plants. He thinks he has worked out the details of the method so as to insure quantitative accuracy. One cannot see how it will lead to more accurate results than the method described in GANONG'S *Plant physiology* (2d ed., pp. 92-97. 1908). In fact, it seems that THODAY'S experimental error must be greater than GANONG'S, due to the small leaf surface used. We know little about what occurs in a leaf subjected to illumination. As BROWN and ESCOMBE suggest in stating their CO₂ intake method, it may modify the power of various contained compounds to hold water at 100° C. Since the amount of atmospheric CO₂ fixed is the question to be answered, the reliability of the increased weight method must be measured by its agreement with the amount of CO₂ taken up under like conditions. It would seem as though the work better be done on perfecting the CO₂ intake method, if indeed BROWN and ESCOMBE did not leave it so. This method is entirely independent of asymmetry, of variation of surface with insolation, and of translocation and changes in the water-holding powers of the leaf. It also measures directly the thing sought. THODAY depended upon the horn hygroscope as a means of determining the condition of stomata. The results obtained with this instrument are at best only indirect and qualitative, as LLOYD³⁷ has suggested. The direct and accurate method devised by LLOYD is certainly preferable.—WILLIAM CROCKER.

³⁶ THODAY, D., Experimental researches on assimilation and respiration in the open air. Proc. Roy. Soc. London B 82:421-450. 1910.

³⁷ LLOYD, F. E., Physiology of stomata. Publ. 82, Carnegie Institution. 1908.

Syndiploid nuclei.—In 1904 NĚMEC³⁸ showed that in vegetative tissues the nuclei of binucleate or multinucleate cells may fuse, giving rise to what STRASBURGER has called syndiploid nuclei and cells. In such cells the mitoses show a correspondingly high number of chromosomes, but in some cases the syndiploid condition disappears from the meristematic zone, and NĚMEC believed that a reduction of chromosomes had taken place. In a preliminary note³⁹ he mentions two kinds of reduction figures: one characterized by chromatin tetrads which split so that bivalent chromosomes arrive at the poles; in the other the diploid number appears suddenly without any tetrads, perhaps due to a fusion of chromosomes.

In chloralized roots tips of *Vicia Faba*, syndiploid cell rows are quite numerous in the lateral rootlets, but such rows often end blindly and are replaced by diploid rows. This may happen in different ways. A syndiploid row may be replaced directly by a diploid one, and in this case it is probable that a reduction of chromosomes has taken place; or the syndiploid initials may die and neighboring cells may crowd in; or peripheral syndiploid initials may cease to function. In these three ways it may come to pass that the lateral root may finally consist of only diploid cells.

It must be remembered that, while binucleate and multinucleate cells are rather common in plants, the syndiploid condition has as yet been studied almost exclusively in chloralized material.—CHARLES J. CHAMBERLAIN.

Sporogonium of Conocephalum.—Miss GRAHAM,⁴⁰ studying *Conocephalum conicum* (*Fegatella conica*), finds that at Ithaca, N.Y., the gametophores begin to appear in June, that fertilization takes place about the first of July, that the spores are fully formed before the beginning of winter, and that in the following May the gametophore stalk rapidly elongates. This elongation is quickly followed by the elongation of the stalk of the sporogonium. The venter of the archegonium is two-layered at the time of fertilization, and soon becomes a massive calyptra. The first division of the fusion nucleus gives rise to two free nuclei, which may lie parallel with or transversely to the major axis of the archegonium. A cell wall is not laid down until some little time has elapsed after division of the fusion nucleus; when the wall appears, it is transverse. By successive transverse divisions a filament of four or five cells is formed. This observation differs from that of CAVERS, who described an octant stage; the reviewer's observations agree with those of Miss GRAHAM. The first longitudinal walls appear in the outer or capsule end of the filament.

³⁸ NĚMEC, B., Ueber die Einwirkung des Chloralhydrats auf die Kern- und Zellteilung. Jahrb. Wiss. Bot. 39:645-730. figs. 157. 1904.

³⁹ ———, Ueber das Schicksal der syndiploid Kerne und Zellen. Ber. Deutsch. Bot. Gesell. 29:113-115. 1910.

⁴⁰ GRAHAM, MARGARET C., Development of the sporogonium and adjacent tissues of the gametophore of *Conocephalum conicum*. Bull. Torr. Bot. Club 36:615-625. pls. 30-33. 1909.

At the time of separation of the mother cells, the growth of the capsule is checked, while the calyptra continues growth, leaving quite a space between capsule and calyptra. The capsule and seta soon resume growth, fill the cavity, and distend the calyptra. No pseudoperianth, such as is found in *Marchantia*, is present. A sheath, which is a specialized portion of the gametophore, invests the calyptra.—W. J. G. LAND.

Evaporation measurements.—The porous cup atmometer is now recognized by ecologists as one of the best instruments for measuring the evaporating power of the air, which is perhaps the most important climatic factor, or set of factors, in determining the vegetation of any locality. One difficulty in its operation has been that rain falling upon the exposed cup penetrates to some extent into the reservoir and vitiates the readings immediately following. To obviate this difficulty LIVINGSTON⁴¹ has devised a rain-correcting atmometer with a mercury valve preventing any water from entering the reservoir. He also emphasizes⁴² the importance of using nothing but the purest distilled water in the instrument and of standardizing the cups at frequent intervals. Recognizing the necessity of some uniform unit of standardization, in order that the results of the various workers may be comparable, he proposes that the standard cup be one that loses water at the same rate as 45 sq. cm. of water surface exposed in a Petri dish 1.5 cm. high and kept constantly filled to the depth of 3 mm. Microorganisms in the cups may be prevented by rinsing the cups and reservoirs with weak mercuric chlorid solution. It has also been found desirable to operate two or more cups at each station, as accidents are not likely to occur simultaneously to all, and thus an unbroken record is made more probable.—GEO. D. FULLER.

⁴¹ LIVINGSTON, B. E., A rain-correcting atmometer for ecological purposes. *Plant World* 13:79-82. 1910.

⁴² ———, Operation of the porous cup atmometer. *Plant World* 13:1111-1119. 1910.



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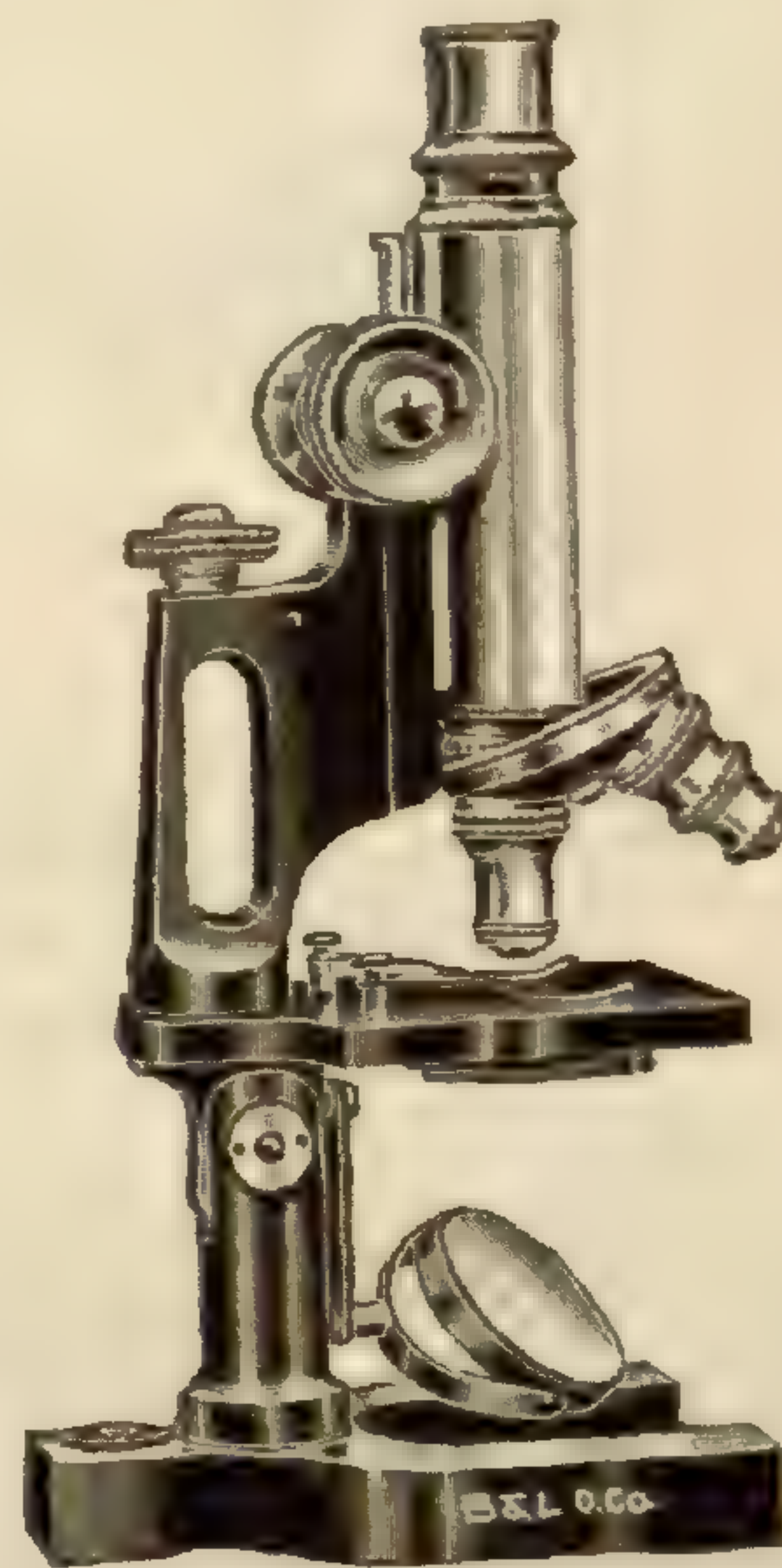
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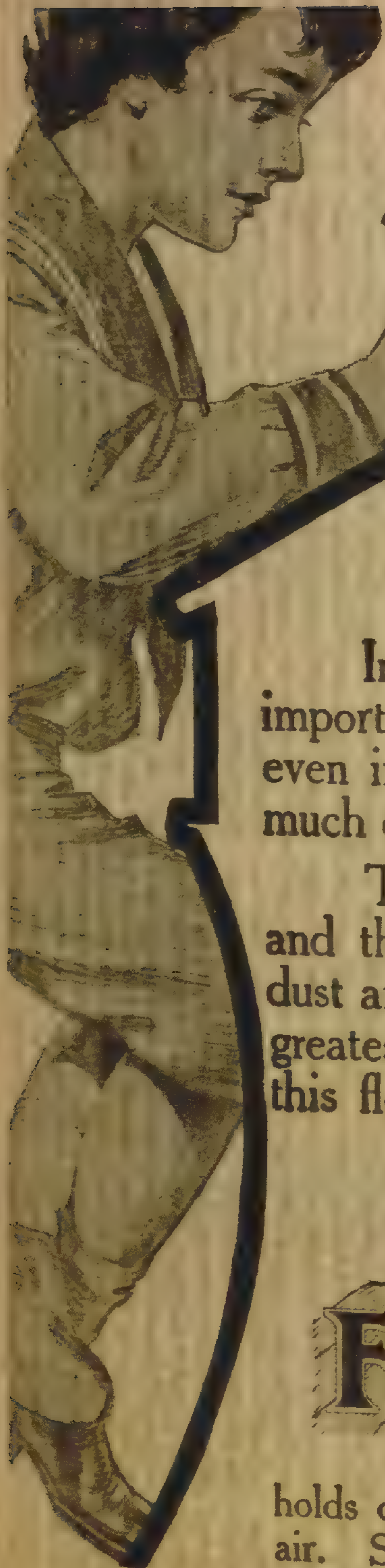
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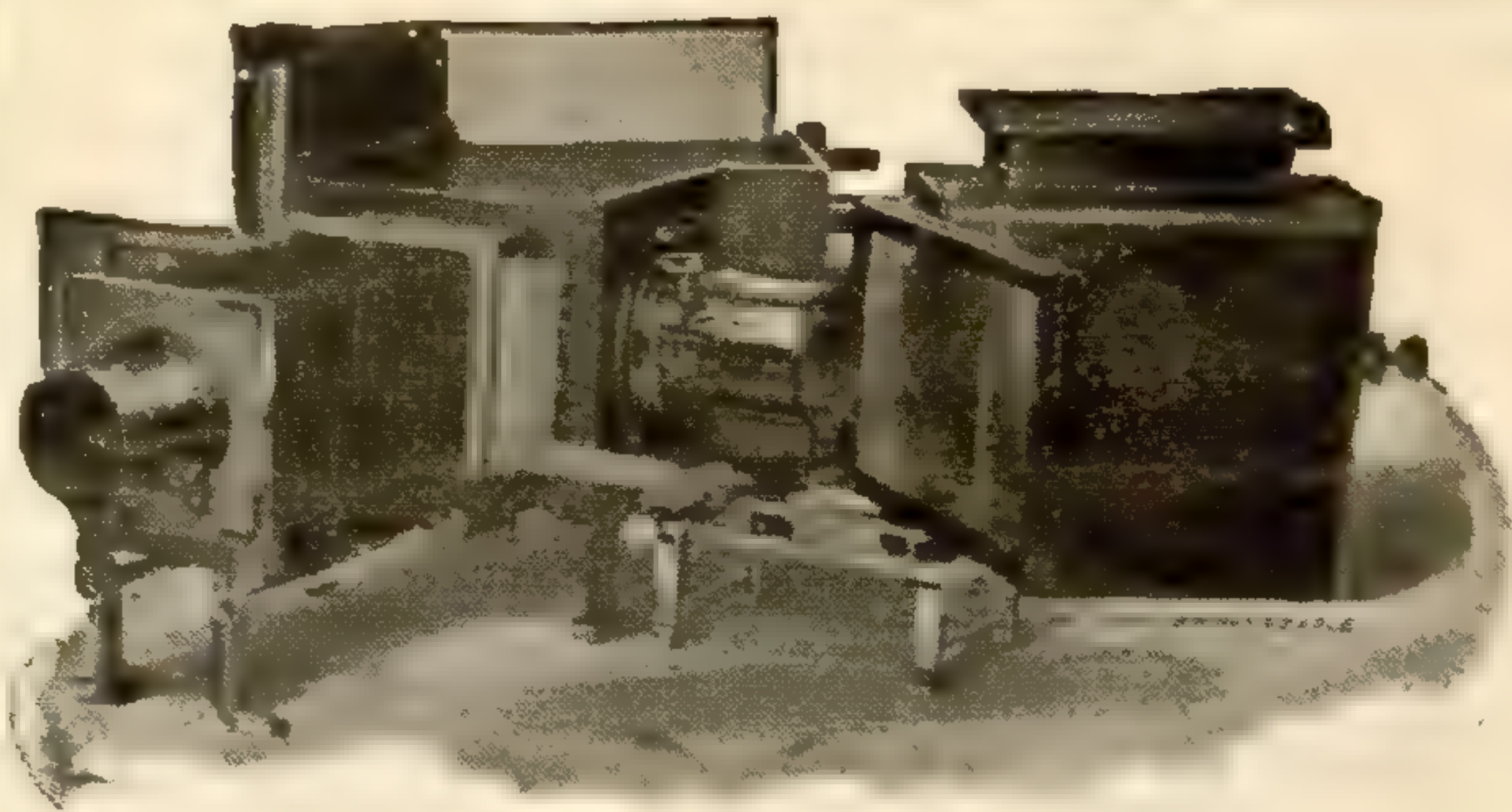
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THE
BOTANICAL GAZETTE

MARCH 1911

THE CAUSES OF VEGETATIVE CYCLES¹

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 143

HENRY C. COWLES

1. The demonstration of vegetative cycles

The work of the past decade has shown most clearly that there are cycles of vegetation, which are comparable precisely to cycles of erosion; in each there is a period of youth, which is characterized by vigor of development and by rapidity of change; in each there is a period of maturity, and finally one of old age, which is characterized by slowness of transformation and by approach to stability, or at least to equilibrium. At the close of the vegetative cycle there is no such universal feature as the base level of the physiographer, since the final vegetative aspect varies with the climate, and hence is called a climatic formation. In the eastern United States, the final stage is a mesophytic deciduous forest; farther to the north and in the Pacific states, it is a coniferous forest; in the great belt from Texas to Saskatchewan, the final stage is a prairie; and in the arid southwest, it is a desert. In every case, the ultimate or climatic plant formation is the most mesophytic which the climate is able to support in the region taken as a whole. In a prairie climate there may be trees, but they occur for the most part near lakes or streams, or in protected depressions, and in the base-leveling of the region they give way to the prairie; quite the same may be said of trees in a desert climate.

It has been ascertained that the original plant formations in any habitat give way in a somewhat definite fashion to those that come

¹ Address delivered as retiring president of the Association of American Geographers, Pittsburgh, December 29, 1910.

after. Pioneer formations usually are hydrophytic or xerophytic, mostly xerophytic in arid climates, and more equally divided in moist climates. For example, the last retreat of the glacial ice left in our northern states a vast tract made up essentially of hills and hollows, the hollows, if deep enough, with lakes. The first vegetation of the hills was xerophytic, and the first vegetation of the hollows, hydrophytic. Finally, except on the higher hills and in the deeper hollows, these first plant formations gave way step by step to the climatic tundra, and, as the climate became ameliorated, this in turn gave way to climatic coniferous forests, and then to climatic deciduous forests as they exist today. So far have the higher hills and the deeper hollows lagged behind the less extreme habitats in their development that there are still to be found many places which continue to have pioneer formations, though, of course, they differ greatly from the original pioneer formations of the tundra.

While the general trend of vegetation is from diversity toward uniformity, it must not be supposed that complete similitude is ever reached even under like climatic conditions. There are species, for example, in the culminating forest of New England which do not occur in Ohio, and species in Ohio which do not occur in Illinois; southward the difference is even more pronounced. And yet it cannot be denied that from the Maritime Provinces to Minnesota and south to the coastal plain the ultimate forest in its larger features is of a single type; the percentages and even the kinds of dominating trees may differ, but the aspect is essentially the same. Much more diverse from one another than are the beginnings or the ends are the intervening stages. Our northern lakes, for example, differ much less from one another in their floristic composition than do the swamps to which they give rise. The initial stages of a rock upland in Tennessee and in northern Michigan are much alike, both in aspect and in floristic composition; the terminal stages in these two widely separated districts are even more alike, but the intermediate stages are very different, northern Michigan having nothing at all comparable to the oak stages in the vegetational development of eastern Tennessee, and the latter region being without the complex coniferous stages of northern Michigan.

In this instance it is likely that some of the northern coniferous stages correspond to some of the southern oak stages; thus we may speak of *alternative* or *substitute* stages, when different plant formations occupy equivalent places in a successional series.

In a desert climate an upland may exhibit almost no succession, since the original xerophytic formation may remain with but little change; in comparison with a successional series in a mesophytic climate, one may speak here of the *elimination* of certain stages. In marked contrast to the lack of succession or to the slow succession on a desert upland is the rapid succession on uplands in humid climates; indeed, it is possible here for mesophytes to exist side by side with xerophytes in the pioneer stages—in such a case one may speak of *telescoped* successions. Even in a climate like that of the eastern United States, telescoping may take place, as in the successions of rich fallow land and in those which follow the cutting of a mesophytic forest. With this brief survey of recent progress in the field of physiographic ecology, we may pass to a similarly brief consideration of the historical development of vegetative dynamics, and then to a consideration of the main theme of the address.

2. The development of dynamic plant geography

The systematic exploitation of developmental or dynamic plant geography presupposes the establishment of the principles of dynamic geology and of organic evolution; hence it could not have antedated LYELL, who brought general recognition of the former, or DARWIN, who brought general recognition of the latter. Results frequently lag far behind their causes, and it is only now, a full half-century after the publication of DARWIN'S *Origin of species*, and three-quarters of a century after the appearance of LYELL'S *Principles*, that the dynamic method is coming to be regarded as the most fundamental thing in plant geography. As in other branches of science, there have been prophets far in advance of their time, though it is only within the last decade that the prophetic insight of these pioneers has had recognition. LYELL records the struggle of the developmental idea in geology, as opposed to the ruling theories of special creation or catastrophism, noting especially the keen philosophy of certain ancient Greeks

and the renascence of these views in Italy through the influence of LEONARDO DA VINCI and of other great contemporaries and followers.

So far as we know, the beginnings of dynamic plant geography are much more recent than are the beginnings of dynamic geology, nor is this strange, since it is easier to recognize the destruction of land by waves and the deposition of material by rivers than to observe the more silent transformation of one plant association into another. Doubtless the earliest observers of such transformations failed to record the things they saw. It is hardly to be doubted, for example, that long ago many a philosophic woodsman must have noted, when he cut down the trees of a forest, that there sprang up a new vegetation differing from the old, and that gradually these first trees of the newly developing forest were displaced by other trees; and there may have been some who were keen enough to see that, after a long time, there was a return to the primeval type of forest.

The earliest account which I have discovered that clearly deals with vegetative dynamics is in a short paper in the *Philosophical transactions* in 1685, in which WILLIAM KING (1) gives a good account of the origin of bog vegetation from floating mats; many times since, this has been reported as an original discovery. Perhaps the first to have a real glimmer of the doctrine of succession, as understood today, was the great French naturalist BUFFON. Although better known for his splendid descriptions of animals, BUFFON in his earlier life was much interested in forestry, and in 1742 he noted (2) that poplars precede oaks and beeches in the natural development of a forest. As a result of this observation, he gave the important advice to foresters that if they wished to cultivate beeches, they should plant them not in the open, but in the shade of those trees which they naturally succeeded. BIBERG (3), a student of the great LINNAEUS, published his thesis in 1749, and in this he describes the gradual development of vegetation on bare rocks; here he observes accurately the pioneer activity of the lichens and mosses, and he notes as well the importance of *Sphagnum* in the development of bogs.

The seeds planted by BUFFON and BIBERG fell on sterile soil; in

France it was observed that BUFFON was trespassing on theological grounds, and he was obliged to recant any views which implied that the world was not made in the beginning once for all; in Sweden the influence of LINNAEUS was wholly against anything dynamic; he never published anything dynamic himself, and when a student like BIBERG set his face in that direction, the master frowned, and said that the student was departing from the true mission of the botanist. It is not strange, therefore, that there followed a sterile period of three-quarters of a century. Yet it was within this period that plant geography was first recognized as a definite branch of science, for this was the period of HUMBOLDT. This also was the period of JOACHIM SCHOUW, who published the first general plant geography, and of the older DECANDOLLE, who gave the weight of his great name to several important treatises in the new subject. But none of these men, not even HUMBOLDT, were permeated with the dynamic principle, so far at least as plant geography is concerned. They placed descriptive plant geography on a solid foundation, and gave it such momentum that for a full century it dominated the entire field of plant geography; indeed in certain places it dominates plant geography today.

France, so often the birthplace of great ideas, gave the pendulum an impulse in the right direction. The sane influence of BUFFON had not altogether been suppressed by the theologians, and finally there arose such men as JUSSIEU, who introduced a flexible natural system of plant classification, which finally displaced the rigid artificial system of LINNAEUS, thus making possible the development of evolutionary theories; such men as LAPLACE, who conceived a theory of planetary evolution, thus making possible the development of evolutionary theories in other lines of science; and such men as LAMARCK and GEOFFROY STE. HILAIRE, who propounded evolutionary theories in biology. The birth of dynamical conceptions in France a century ago rejuvenated science throughout Europe, making possible the development of a LYELL and a DARWIN. It also made possible the development of a dynamic trend in the new science of plant geography, though, as previously noted, the momentum given to descriptive geography was too great readily to be overcome.

Very properly the first work of the new period along dynamic lines was done in France; in 1825 DUREAU DE LA MALLE (4) published the first paper which gave the results of a careful study of plant succession involving the observations of a number of years. His work was done mainly in cut-over areas of forest, and no work done since greatly surpasses it in accuracy and thoroughness. The marvelous clear-sightedness of DUREAU DE LA MALLE is well shown in the title of his chief contribution, which (in English rendering) is: "Memoir on alternation or on alternative succession in the reproduction of plant species living in association (*société*)—is it a general law of nature?" DUREAU DE LA MALLE (not STEENSTRUP, as frequently supposed) first used the term succession in the present sense; probably he was the first also to use the term society as an expression of plant grouping. The year 1845 is a noteworthy one because it was then that EDWARD FORBES gave a short paper (6) before the British Association, opening up an entirely new line of study, namely, the interpretation of past geographic features by the present. He was the first to understand the significance of endemism in relation to previous connections between islands and continents that now are isolated.

In 1841 a great advance was made by the Danish geologist STEENSTRUP (5), who discovered the possibility of using the fossils of the immediate (i.e., postglacial) past as a means of interpreting the climatic changes and the correlated vegetation changes of recent epochs. VAUPELL, a student of STEENSTRUP, but more botanically inclined, applied his ideas in detail (7, 9), and in the years between 1851 and 1863 gave to the world his famous account of the postglacial development of Danish vegetation, showing that the birch was the chief early pioneer, and that later it was followed in turn by the pine and the oak, and finally by the beech, which dominates today. From 1856 to 1859 REISSEK (8) worked out the dynamical development of the vegetation on the islands of the Danube. In 1876 GREMBLICH (10) seemed to realize the actuality of cycles of vegetation. In 1881 HULT, a Finnish botanist, made the first comprehensive study of succession (11) as it is now taking place in a given region, and he was the first to recognize that a comparatively large number of pioneer plant associations later

give way to a comparatively small number of relatively permanent associations.

In 1888 TREUB, whose recent premature decease we so keenly regret, began the study of the new vegetation of Krakatoa (12), thus inaugurating one of the most fruitful lines of investigation in dynamic plant geography. In 1891 WARMING, to whom more than to any other we owe the present large place occupied by ecological plant geography, published the first of his developmental studies of Danish dune vegetation (13). This was followed by a similar treatment of the Rhône delta by FLAHAULT and COMBRES (14), and of the North German heath by GRAEBNER (16), and also by WARMING's *Plantesamfund* (15), the original Danish edition of his well known *Plant geography*, in which there is much material of dynamic import, together with the formulation of a number of "laws of succession." In 1896 MEIGEN (17) made a systematic study of succession, somewhat along the lines previously followed by HULT, and he showed that there is a final tendency toward equilibrium. This brings us to the period in which dynamic plant geography was taken up actively in this country, and here our historical résumé may well give place to the main topic of this paper.

3. The delimitation of successional factors

No systematic attempt has been made hitherto to group in an analytic manner the phenomena of succession from the standpoint of their causation. WARMING (15) made a great advance toward this end by gathering together the known records of vegetative change or succession; he noted that vegetative change is particularly evident on new soil (as along sandy shores, and in marshes, on lava, on landslip soil and talus, and on burned and fallow land). He summarizes his studies by giving six laws appertaining to succession. CLEMENTS (21) attempted to distinguish between primary and secondary successions, the former being those on newly formed soils, and the latter those on denuded soils. This classification seems not to be of fundamental value, since it separates such closely related phenomena as those of erosion and deposition, and places together such unlike things as human agencies and the subsidence of land. CLEMENTS, like WARMING, gives a summary of results in the form of laws.

While most observers very properly have paid chief attention to the actual facts of succession rather than to their underlying causes, a scrutiny of past results shows very clearly that the phenomena considered have differed greatly in kind. Obviously the phenomena of bog development, as observed by WILLIAM KING, had to do with a succession in which the activities of the plants themselves played the leading part; the humus accretions of the bog plants, such as the peat moss *Sphagnum*, made possible the development of another vegetation on a higher soil level. In a comparable manner, the successions observed by BUFFON, by BIBERG, and by DUREAU DE LA MALLE had to do with plant activities; the forest trees of a given generation cast the shade necessary for the development of other trees which need shade rather than light for their development; BIBERG's lichens accumulated a soil which made possible the development of higher vegetation on rock surfaces. STEENSTRUP, however, in his study of the fossils, introduced to the scientific world a new kind of succession phenomena, for in his elucidation of the postglacial history of Denmark there were recorded changes of broader significance than those hitherto observed; it was clear that the transition from the tundra vegetation through the birch and pine vegetation to the oak and beech, as developed by him and by his student VAUPELL, was a record of climatic change, inasmuch as the very same horizontal succession may be observed today in journeying from northern Scandinavia to Denmark. A third and equally diverse kind of succession phenomena was recorded by REISSEK in his study of the islands in the Danube, for here there was clearly recognized the influence of physiographic change on vegetation. Thus in succession we may distinguish the influence of physiographic and of biotic agencies. The physiographic agencies have two aspects, namely, regional (chiefly climatic) and topographic.

4. Regional successions

Regional successions are so slow in their development that they can be studied almost alone by the use of fossils. Hence the experimental method, which has proven so potent in unraveling many a biological tangle, is here of no avail. It is not strange, therefore,

that these successions are and probably must remain the least understood of all. There are, perhaps, four great examples of extensive regional change, which may be accepted as demonstrated, namely: (1) the change from the Carboniferous to the Permian, which is made evident particularly through the replacement of the carboniferous ferns, fern allies, and primitive gymnosperms by the *Glossopteris* flora and later by the modern gymnosperms; (2) the subordination of the gymnosperms to the angiosperms in the Cretaceous; (3) the elimination of tropical forms in boreal regions in the late Tertiary; and (4) the postglacial invasion of southern forms into boreal regions accompanying and following the retreat of the glacial ice. Generally it is held that the dominating factor in these vegetative successions is climatic change, and that this climatic change is chiefly one of temperature. Of this there can be no doubt in the case of the changes immediately before and after the Pleistocene ice invasion. The constant relation between glaciation and the development of the *Glossopteris* flora in the Permian makes it likely that the general vegetative changes of that epoch also were due primarily to temperature.

On the whole, however, there has been a general tendency to overestimate the influence of temperature as an ecological factor. The trend of nearly all experiment has been to show that water is of vastly greater importance, and it well may be that the change from the atmospheric humidity which seems to have characterized the Carboniferous to the aridity which seems to have characterized the Permian had more to do than did the decreased Permian temperatures with the elimination of the carboniferous flora and with its replacement by mesozoic forms. The most puzzling of the great vegetative transformations of the past was the sudden change from the dominantly gymnospermous forests of the Jurassic to the domination of the world by angiosperms in the Cretaceous. We know that after the Permian there was a gradual climatic amelioration toward genial conditions similar to those which characterized the Carboniferous; this amelioration seems to have culminated in the Cretaceous, which, like the Carboniferous, was also a period of extensive base-leveling. Very probably the high temperatures and the great atmospheric humidity of the Cretaceous gave con-

ditions that particularly favored the angiosperms, which as a group are much more mesophytic than are the gymnosperms.

To summarize on regional successions, it would seem that secular changes in climate, that is, changes which are too slow to be attested in a human lifetime, and which, perhaps, are too slow to be attested in a dozen or a hundred lifetimes, are the dominating factors. It is possible that these changes sometimes are more rapid than at other times, and there are those who would have us believe that the climate now is growing warmer, as witness the rapid recession of many of our North American glaciers; there are others who are quite as sure that the climate is growing colder, as witness the southward retreat of the "timber line" in Scandinavia. Still others feel equally confident that the recession of glaciers is due to increasing aridity; this explanation has the advantage also of accounting for retreating "timber lines." And there yet remain some who believe that all such changes may be of short duration, as it were cycles within cycles, or feeble and short-lived oscillations of great climatic waves. It is to be pointed out that great earth movements, either of elevation or subsidence, that is, the far-reaching and long-enduring epeirogenic movements, as contrasted with the oscillations of coast lines, must be considered in accounting for regional successions; the elevation of the Permian and the base-leveling of the Cretaceous must have played a stupendous part in instituting vegetative change.

5. Topographic successions

In striking contrast to secular successions, which move so slowly that we are in doubt even as to their present trend, are those successions which are associated with the topographic changes which result from the activities of such agents as running water, wind, ice, gravity, and vulcanism. In general these agencies occasion erosion and deposition, which necessarily must have a profound influence upon vegetation. I have considered in another place and in some detail (18, 19, 20) the influence of most of these agencies, and it will suffice in this place to summarize a few of the leading kinds of phenomena that are involved. As might be expected, the influence of erosion generally is destructive to vege-

tation, or at least retrogressive (i.e., tending to cause departure from the mesophytic), while the influence of deposition is constructive or progressive (i.e., tending to cause an approach toward the mesophytic). Progressive successions are well illustrated in the development of flood plains along rivers, and in the growth of sandy shores; retrogressive successions are associated with the eroding activities of streams and of receding shores.

Sometimes erosion may not have a retrogressive influence and sometimes the effect of deposition is not progressive. For example, on a somewhat rapidly eroding clay cliff of Lake Michigan, there often occur certain xerophytic annuals, which develop during the comparatively stable summer period, and a few perennials, such as the sumac and *Equisetum*, which have underground organs that enable them to migrate landward as fast as the cliff recedes; here we have a remarkable instance of rapid topographic change without a corresponding plant succession, either progressive or retrogressive. A marked increase in erosive intensity would destroy all vegetation, and a marked decrease in erosive intensity might institute a progressive vegetative succession. Deposition unaccompanied by progressive changes may be illustrated by an instance from the Lake Michigan sand dunes. Frequently a growing dune is inhabited by xerophytic annuals and by a few shrubs or trees (as various willows and the cottonwood); such a place illustrates the extreme of topographic dynamics, but often the vegetation is static. A great increase in depositional intensity results in the destruction of all the plants, while a decrease in depositional intensity results in progressive succession. Retrogression or a static condition of vegetation is to be seen also along rapid streams, where there is a considerable deposition of coarse material. A striking illustration of retrogression associated with deposition is afforded by lava flows.

6. Biotic successions

A. GENERAL FEATURES

Of less interest, perhaps, to the physiographer than are the vegetative changes hitherto considered, but of far greater import to the plant geographer, are the vegetative changes that are due to

plant and animal agencies. These are found to have an influence that is more diversified than is the case with the physiographic agencies; furthermore, their influence can be more exactly studied, since they are somewhat readily amenable to experimental control, but particularly because they operate with sufficient rapidity to be investigated with some exactness within the range of an ordinary lifetime. If, in their operation, regional agencies are matters of eons, and topographic agencies matters of centuries, biotic agencies may be expressed in terms of decades.

It has been seen that changes of climate or of topography generally institute vegetative changes; indeed this would have been predicted to be the case, even without examination. But at first thought it seems somewhat striking that far-reaching vegetative changes take place without any obvious climatic change and without any marked activity on the part of the ordinary erosive factors. Indeed, it is probably true that the character of the present vegetative covering of the earth is due far more to the influence of these relatively silent and subtle factors than to the more obvious factors previously considered. So rapid is the action of the biotic factors that not only the climate, but even the topography may be regarded as static over large areas for a considerable length of time. It has been said that many of our Pleistocene deposits exhibit almost the identical form which characterized them at the time of their deposition; in other words, the influence of thousands of years of weathering has been insufficient to cause them to lose their original appearance. These thousands of years would have sufficed for dozens and perhaps for hundreds of biotic vegetative cycles. Many a sand dune on the shores of Lake Michigan is clothed with the culminating mesophytic forest of the eastern United States, and yet the sand dunes are products of the present epoch; furthermore, sand is regarded generally as a poor type of soil in which to observe rapid succession. If a clay upland were denuded of its forest and its humus, it is believed that only a few centuries would suffice for the mesophytic forest to return.

From the standpoint of dynamic plant geography our land areas are divided into two well marked categories: on the one hand is the erosion topography that is characteristic of the eroding and

depositing phases of present streams and shores, and on the other hand is the *pre-erosion* topography (as it may be termed) which is characteristic of those areas that have not as yet been invaded by erosive forces. In our northern states the areas characterized by the presence of a pre-erosion topography often greatly exceed in extent the areas which are characterized by an erosion topography. South of the glaciated region, however, the areas characterized by the presence of an erosion topography often greatly dominate. But the influence of biotic agencies is not confined to areas that are characterized by a pre-erosion topography. For example, in our eastern forested region the development of a ravine, which furnishes a characteristic illustration of rapid topographic dynamics, exhibits only here and there actual erosion or deposition; the ravine slopes as a whole are covered with a mesophytic vegetation, because at a given spot the interval between periods of active erosion often is sufficiently long to permit the development of an entire biotic cycle. Perhaps in no other way could there be brought out more strikingly the durational contrast between topographic and vegetative cycles; a ravine is an index of extreme topographic youth, and yet in its development there is ample time for the complete development of many vegetative cycles. Quite as in ravines, the cliffs of streams and shores often exhibit temporary exemption from erosion, whereupon there is at once instituted a biotic cycle, which often has sufficient time for complete development before erosion again becomes active.

B. THE HUMUS COMPLEX

a. Water.—It is now time to consider the varying aspects of the biotic agencies which institute succession. Of these the first to be mentioned, because of its unquestioned supremacy, is the accumulation of humus. There are a number of different ways in which the accumulation of humus affects the trend of succession. It can scarcely be doubted that the most important of these humus influences, and perhaps the most important of all influences, inheres in the change which the humus brings about in the water relation of the soil. Speaking generally, humus accumulation occasions an increase in soil moisture on uplands and a decrease in

soil moisture in depressions; hence it is probable that the changed water relation due to humus accumulation is the dominating factor in determining the mesophytic trend, both in hydrophytic and in xerophytic habitats. Although bare sand supports a xerophytic flora, the accumulation of a thin humus layer is sufficient for forest development, and the Michigan dunes show that the most mesophytic of our forests can grow on a sand dune, if there is present a humus layer a few centimeters in thickness. On rock uplands, lichens commonly are the first humus accumulators; not only do they contribute humus by their own decay, but they give shelter and anchorage to plants of higher order, whose humus-accumulating capacity is greater. As long as the vegetation is open, and the humus exposed to the sun and wind, accumulation is slow, because of oxidation. But when the vegetation cover is more fully developed, the humus is more and more protected and hence accumulates more rapidly.

The relation of swamp successions to humus accumulation is particularly close. For each level both below and above the water table, there is a characteristic plant formation. In the deeper ponds only submersed aquatics can develop, but after a time their humus débris accumulates to such an extent that plants with long stems or leaf-stalks (such as the pondweeds and water lilies) are able to develop. They in turn build up the humus and prepare the way for their own elimination and for the development of such plants as the bulrush, which grows in shallow water. The latter again prepare the way by further humus accumulation for the first land plants, and they again for others. In all this well known successional series, the dominating factor clearly is a decreasing water content due to the accumulation of humus.

b. Soil organisms.—Another important influence associated with humus accumulation is the increase of soil organisms. These may play a part scarcely second to water, but as yet we know all too little of their activities to be certain of their precise place in the scale of importance. We know, however, that nitrogen is one of the essential plant constituents, and that it is made available chiefly by certain bacteria and fungi. Since these forms live on decaying organic matter, it seems likely that humus accumulation

is likely to favor their increasing development and hence an increasing supply of available nitrogen. A single instance will suffice to show the possible importance of soil organisms in succession. The beech, which is a characteristic member of the culminating forest of the eastern United States, has roots which are enveloped by saprophytic fungi; it is believed that these fungi represent the absorptive system of the tree, and it is likely also that they are able to make nitrogen available, since so many similar fungi are now known to possess this power. In any event, the beech is known to depend upon the fungus, being unable to flourish without it. Obviously, then, the beech cannot appear in a successional series until its associated saprophytic fungus finds conditions requisite for its development in the soil. It is likely, too, that other saprophytic organisms are detrimental to various green plants, thus becoming a factor in their elimination. There is opened up here a great field of investigation, and all that can be stated now with definiteness is that it is likely to be demonstrated that the accumulation of humus is of profound significance in the development of successive saprophytic organisms, and probably on this account in the succession of the higher plants.

c. Toxicity.—Still another humus factor that seems likely to be of large significance, but whose exploitation is so recent that we cannot yet appraise it, is soil toxicity. It has been known for a long time that the roots of plants give off various excretions, but it is only through the recent careful work of LIVINGSTON and his associates (22), and later of SCHREINER and REED (25, 26), that we have come to know much concerning their nature and influence. In the case of wheat it has been ascertained that the roots give off certain substances which are deleterious and perhaps actually toxic, especially to wheat. Such results should not occasion surprise, since it is well known that many bacteria excrete substances which retard or even prevent the further growth of their own kind.

One of the greatest puzzles to the student of plant dynamics has been afforded by the successional series in bogs, since in spite of the wet soil there are many plants that obviously are xerophytic. There is universal agreement that there is something in bog soils

which is detrimental to plant growth, but there have been various theories as to its nature. Some years ago LIVINGSTON (23) discovered that bog waters have an effect on the growth of algae which is quite comparable to the effect of various toxic agents. More recently DACHNOWSKI, following the lead suggested by SCHREINER and REED, has been making a careful study of bog toxins (27, 28). On account of the poor drainage of bogs, there is no other habitat where root excretions would be more likely to remain. Year by year these excreta would accumulate, thus making the bog more and more unfitted for the development of ordinary hydrophytes; hence for a time the dominating bog plants would be those which would be able to withstand the acids and other deleterious excreta given off by the roots or produced subsequently by changes in the accumulating humus. However, when these bog xerophytes bring the humus level well above the water table, the deleterious plant products will be more and more oxidized, and ultimately there will be produced a soil of such character that ordinary mesophytes may flourish in it. While there is much in this theory which still requires confirmation, it certainly accounts for most bog phenomena and is not controverted by any known facts. It is likely also that some of the accumulating soil compounds may be of importance in neutralizing deleterious inorganic or organic soil constituents. In any event, the study of soil toxins and of their varied relations to plants is one of the great fields of investigation for the future.

d. Food.—Perhaps there are some who would have supposed that the chief significance of humus accumulation lies in the increased amount of plant food that thus is made available. Once it was supposed that the well known luxuriance of plants in humus is due to the large amount of plant food which it contains. Long ago this luxuriance was shown to be in the main due to other causes, but recent experiments have demonstrated that ordinary green plants are able to absorb certain foods (as glucose), and it may be that such plants actually utilize in this way some of the substances of the humus. It is likely that the increasing food supply in accumulating humus is an important factor in the succession of the soil organisms, but as yet this subject has never been investigated.

It also offers a fascinating field for study. The depletion of mineral foodstuffs in the soil has been urged as a successional factor, but it is doubtful if this is of any consequence. The great abundance of the mineral constituents of plants in nearly all soils is in strong contrast to the minute amounts which the plants contain. Furthermore, the plants in their decay return to the soil the mineral elements which they took from it.

e. Temperature and aeration.—Finally humus accumulation alters the soil temperature and the air content of the soil. For the most part changes in air content and in temperature probably are insufficient to be of great influence in vegetative change. In bogs, however, there is evidence that each of these factors is of importance. TRANSEAU has shown (24) that in the growing season the temperature of the water and of the soil in bogs is below that of other soils, and of the superincumbent air. Such a condition certainly is detrimental to root activity. Similarly TRANSEAU (24) has shown that the lack of aeration in bog soils is detrimental to root activity. Thus for these reasons (and probably also because of soil toxicity, as noted above) certain stages in bogs are characterized by the development of a xerophytic vegetation, since the unfavorable conditions for root absorption make existence in bogs difficult for any plants with aerial organs except such as have structures which reduce transpiration. That such bog plants are actual and not merely apparent xerophytes was demonstrated in brilliant fashion by TRANSEAU (24), who produced plants with xerophytic structures from ordinary plants by growing them in bog conditions.

C. SHADE

Next in importance to humus among the dynamic biotic agencies is shade. The foresters have known for generations that in the reforesting of a region the first trees to appear are those which require a large amount of sunlight for their development; conspicuous among such light-requiring pioneers are the poplars and birches. Rarely is a dense growth of these trees followed by trees of similar kind, since the increasing shade makes the development of seedlings of these species more and more difficult. Other trees, however, perhaps pines and oaks, are able to thrive in a degree of

shade which aspens and birches might not be able to endure. Finally the pines and oaks in turn may be succeeded by such trees as the beech, the sugar maple, and the hemlock, since these trees are able to develop in a considerable amount of shade. The latter trees may continue indefinitely, unless climatic or topographic changes intervene, since, unlike most species of trees, their seedlings are able to develop in shade as dense as that which is cast by the parent trees. While the influence of increasing shade, as here set forth, is undoubted, the extent of its influence is not known; *pari passu* with the increase of shade, and partly on account of it, there goes on the accumulation of humus. On uplands in our climate each of these factors tends to bring about the development of a mesophytic forest, but as yet it is impossible to determine which has the more potent influence. Increasing shade favors the mesophytic trend of upland successions in yet another way than through its direct influence and through its effect upon humus accumulation; the cutting off of light results in increased atmospheric humidity and hence in decreased evaporation. Some recent observations by FULLER (29), as yet unpublished, show that the pioneer plant formations of the Indiana sand dunes are characterized by high evaporation, and that this evaporation progressively decreases until the minimum is reached in the climatic forest.

In contrast to ordinary uplands is the influence of light upon the development of vegetation in lakes. At the outset there are many lakes which are too deep to have a conspicuous vegetation of green plants on the bottom. Through the accumulation of inorganic detritus and of humus, the latter arising from the decay of green plants living in the upper waters and from the decay of other organisms at all levels, there gradually is made possible the development of a plant formation on the bottom, composed of plants which require only a minimum amount of light. In succeeding years the shallowing of the lake makes possible a greater and greater development of green herbage, unless the development of a rich floating vegetation again cuts off the light. It is obvious that the influence of light and shade on succession is not so explicitly related to life as is that of humus; humus can arise only from organisms, but shade may be cast by many other things than trees. The rapid develop-

ment of a mesophytic forest in a canyon is due in large part to the increasing shade which is cast by the walls as the canyon deepens. However, the predominating influence of shade certainly is in connection with forest development, and hence it is not unfair to group it with biotic influences.

D. PLANT INVASION

A further biotic influence is that of plant invasion. In the long period of geologic history, plant migrations from one region to another must have played a tremendous part in the changing aspect of vegetation. There is reason to believe, however, that such changes, apart from those due to human influence, have been wrought almost as slowly as those due to climatic change. So imperceptibly do these migrations take place that we know of no profound change that has been wrought by this means in natural floras within historic time.

E. MAN

The last of the biotic influences to be considered is that of man. Most of the factors hitherto considered, especially increasing shade and accumulating humus with its varied kinds of influence, cooperate to transform originally hydrophytic and xerophytic plant formations into those that are more mesophytic; that is, they institute progressive successions. The influence of man, however, almost without exception, is retrogressive. Human culture reaches its highest expression in mesophytic climates or on mesophytic soils; the xerophytic soils of rocky crags and of sand barrens are unfavorable places for human exploitation, and the desert is for man an unprofitable waste, except where he finds an oasis or makes a district mesophytic through irrigation. Similarly, the waters are of value chiefly as avenues of transportation and as a source of food, not as a habitation; and swampy tracts are considered valueless, unless made mesophytic by drainage. Man, therefore, in seeking a place of abode, in clearing land for agriculture, and in his search for timber, has destroyed chiefly mesophytic vegetation, in other words, the very vegetation which, in most areas occupied by human culture, has been seen to be the culminating plant formation.

When a forest is destroyed by cutting, the succeeding vegetation commonly is more xerophytic than that which was destroyed, because of increased light and decreased humus. The influence of fires is much more retrogressive, because the vegetation of the forest floor, as well as the trees, is destroyed, and also because the humus is more largely oxidized. Both in such areas as these which gradually return to the forest, and in other areas which are prevented from making such return, on account of their use for cultivation, or for habitation, or for grazing animals, there enter among the pioneers a large number of cosmopolitan weeds which follow in the train of man. Most of these weeds are of xerophytic tendencies, and hence are well fitted for these pioneer stages. In the revegetation of fallow land and in reforestation, these immigrants soon disappear, giving way before the returning native forms which inhabited the region before man entered with his destructive axe and torch.

F. PLANT PLASTICITY

Before concluding this section on biotic agencies, there should be noted some instances where dynamics in the habitat meets with a reaction other than that of succession. Very frequently in the draining of a pond by humus accumulation, the same plants may be found in different stages, but characterized by a change of aspect. For example, the mermaid weed (*Proserpinaca*), the water hemlock (*Sium*), and the water smartweed (*Polygonum amphibium*) are fitted for existence in a shallow pond and also in a swamp where the soil level is above the water table. In the former instance the plants possess so-called water leaves, which vary greatly in form and structure from the air leaves, which are seen in the following swamp stage. Such amphibious plants thus have the power through their great plasticity of existing in two distinct plant formations; many of their companions, however, in the two situations are quite unlike, indicating that the habitat range of the latter is narrower, on account of their smaller plasticity.

In the western forests, the Douglas spruce may be a xerophytic pioneer, and yet may remain through all the stages of forest development, including the culminating mesophytic forest; this remark-

able tree may even dominate in each of the stages. The Douglas spruce differs from the amphibious plants in that it exhibits no such striking changes in leaf habit in the different conditions in which it lives; however, the change in the accompanying vegetation is much more profound than in the swamp, for at the outset the Douglas spruce may be accompanied by xerophytic pines and junipers, and at the close by the mesophytic hemlock and by a luxuriant carpet of mesophytic ferns and mosses. Thus it is clear that the life range of some plants is very broad and of others very narrow; obviously the latter are the best markers of habitat dynamics, for with a change of conditions they soon give way to other forms. Of especial interest to the physiologist is the situation in such plants as the Douglas spruce, whose leaves without change of form or structure seem equally fitted for light or shade, for dryness or humidity.

7. Conclusion

It is not to be supposed that all the influences which are involved in plant succession have been outlined in the preceding pages. Indeed, some minor contributory factors have been purposely omitted, because of the brief time allotted upon such an occasion. However, it is to be hoped that the dominating factors, so far as known at present, are here mentioned. From a survey of the various agencies involved, it seems clear that the influences which bring about succession differ profoundly in their nature, and also in the rapidity of their action. Although they grade into one another as do all phenomena of nature, we may recognize climatic agencies, which institute vegetative cycles whose duration is so long that the stages in the succession are revealed only by a study of the record of the rocks. Within one climatic cycle there may be many cycles of erosion, each with its vegetative cycle. The trend of such a cycle can be seen by a study of erosive processes as they are taking place today, but the duration of the cycle is so long, that its stages can be understood only by a comparison of one district with another; by visiting the parts of a river from its source to its mouth, we can imagine what its history at a given point has been or is to be. Within a cycle of erosion there may be many vegetative cycles, and among these are some whose duration is so

short that exact study year by year at a given point makes it possible to determine not only the trend of succession, but the exact way in which it comes about. We can see one stage replacing another before our eyes, and hence we may hope some day, if we exercise sufficient ingenuity and patience, to understand the underlying causes of the change. It is clear therefore that vegetative cycles are not of equal value. Each climatic cycle has its vegetative cycle; each erosive cycle within the climatic cycle in turn has its vegetative cycle; and biotic factors institute other cycles, quite independently of climatic or topographic change. It is small wonder that within this complex of cycle within cycle, each moving independently of the others and at times in different directions, dynamic plant geography has accomplished so little in unraveling the mysteries of succession. It may be some small contribution to this end, if the preceding considerations assist in delimiting the problems.

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STUDIES ON JAMAICAN HYMENOPHYLLACEAE

FORREST SHREVE

(WITH EIGHT FIGURES)

The Hymenophyllaceae, or filmy ferns, are one of the most hygrophilous groups of terrestrial plants, and possess a number of features of anatomy and physiology in common with aquatics and the bryophytes. Although mainly restricted to tropical and subtropical regions with heavy rainfall and to habitats of high humidity, yet some of the species grow as epiphytes in company with bromeliads and succulent orchids, a fact which attracted the writer to a study of their local distribution and the gross physiology of their relation to water supply and atmospheric humidity.

The results presented in this paper were secured at the Tropical Station of the New York Botanical Garden at Cinchona, Jamaica, chiefly during the spring of 1906, while the writer was holding the Adam T. Bruce Fellowship in the Johns Hopkins University, and partly in the summer of 1909 during several months' absence from the Desert Laboratory. Cinchona is at an altitude of 1525 m. and is hard by the virgin rain forest, in which the Hymenophyllaceae attain to a wealth in species and individuals which cannot be far surpassed in any other place in the world. Of the 459 species credited to the family by CHRISTENSEN in the *Index Filicum*, 49 occur in Jamaica, and 34 of these have been available for study and observation.

Distribution

VERTICAL AND REGIONAL DISTRIBUTION IN JAMAICA.—JENMAN¹ lists for Jamaica 23 species of *Hymenophyllum* and 26 of *Trichomanes*. For 31 of the total number of species he states the vertical distribution as based on his long experience in collecting in various parts of the island. His statements indicate that there are but 5 species found only below 915 m. altitude, and 17 found only

¹ JENMAN, G. S., Synoptical list of Jamaican ferns. Bull. Bot. Dept. of Jamaica, nos. 18 and 20. 1890.

above 1220 m. The number of species (of the 31) to be expected at the different altitudes is as follows:

305 m.	610	915	1220	1525	1830	2135
10	19	19	21	31	27	20

It is in the unbroken forests of the windward slope of the Blue Mountains, at about 1525 m. altitude, that the Hymenophyllaceae are richest in species, and it is there too that they are most numerous in individuals, forming a far more conspicuous element of the vegetation than at higher or lower elevations. The most abundant and characteristic species at 1525 m. are:

Hymenophyllum fucoides Sw. ²	Hymenophyllum catherinae Hook.
Hymenophyllum asplenioides Sw.	Trichomanes crispum L.
Hymenophyllum ciliatum Sw.	Trichomanes rigidum Sw.
Hymenophyllum polyanthos Sw.	Trichomanes crinitum Sw.
Hymenophyllum lanatum Fee	Trichomanes radicans Sw.
Hymenophyllum axillare Sw.	Trichomanes pyxidiferum L.
Hymenophyllum lineare Sw.	Trichomanes capillaceum L. (<i>T.</i>
Hymenophyllum sericeum Sw.	<i>trichoideum</i> Sw.)

In virgin forest along the banks of the Mabess River, at about 1100 m. altitude on the windward side of the island, the writer has seen rich growths of Hymenophyllaceae, which were made up, however, solely of *Trichomanes Hookeri* Presl. (*T. muscoides* Sw.) and *T. pyxidiferum* L. Near the summit of Mount Diablo, at 600 to 700 m. altitude in the central limestone district of Jamaica, the Hymenophyllaceae are relatively rare, and must be sought carefully to be found at all. The only species observed there by the writer were:

Hymenophyllum hirtellum Sw.	Trichomanes crispum L.
Trichomanes Hookeri Presl.	Trichomanes arbuscula Desv. (<i>T.</i>
Trichomanes sphenoides Kze.	<i>Bancroftii</i> Hook. & Grev.)

² The nomenclature used is that of CHRISTENSEN's *Index Filicum*. The writer's collection of Hymenophyllaceae was determined by the late Dr. L. M. UNDERWOOD of Columbia University.

The writer has been told by Mr. WILLIAM HARRIS that in collecting at Dolphin Head, in the extreme west end of Jamaica at 550 m. altitude, he observed only two species:

Trichomanes sphenoides Kze.

Trichomanes arbuscula Desv.

On passing upward in the Blue Mountains from 1525 m., the Hymenophyllaceae are found to become fewer in both species and individuals. There is but a single form found only above 1830 m. (*Hymenophyllum antillense* Jenm.), while other species common and characteristic above this altitude are:

Hymenophyllum tunbrigense Sm.

Hymenophyllum lanatum Fee

Hymenophyllum fucoides Sw.

Hymenophyllum hirsutum (L.) Sw.

Hymenophyllum asplenioides Sw.

Hymenophyllum sericeum Sw.

Hymenophyllum polyanthos Sw.

Trichomanes crispum L.

Hymenophyllum lineare Sw.

Trichomanes pyxidiferum L.

Judging by the ten-year rainfall record³ for Blue Mountain Peak (2264 m.) and by hygrograph records obtained by the writer at Sir John Peak (1890 m.), the conditions of rainfall and humidity are no less favorable for the filmy ferns at the higher altitudes than at 1525 m.; indeed the percentage of cloudiness would appear from casual observations to be greater on the highest ridges and peaks. The mean annual temperature at Cinchona is 16° C., while that at Blue Mountain Peak may be closely approximated from a record of the monthly absolute maximum and minimum at that point to be 12° C. Although there are but few alpine features impressed upon the vegetation as a whole at the highest altitudes, yet the less abundance of the Hymenophyllaceae must be referred to the slightly lower range of temperatures rather than to less favorable conditions of rainfall and humidity. The scarcity of species and individuals at low altitudes and at such localities as Mount Diablo and Dolphin Head, in the drier portions of the island, is obviously due to the lower rainfall, humidity, and cloudiness as contrasted with the Blue Mountain forests. Where Hymenophyllaceae occur at all below 915 m., or upon the drier leeward slopes of the Blue Mountains at greater elevations than this, they

³ All climatological data for long periods are taken from the records of the Department of Public Gardens and Plantations of Jamaica.

are confined to spots where the conditions are made favorable by very local topographic or related causes; on rocks near to waterfalls, about the bases of trees in deep shade, and on the lower sides of moss-covered logs the conditions of humidity and water-supply resemble locally the climatic conditions of the mountain forests. The Hymenophyllaceae which occur at low altitudes are chiefly small species of *Trichomanes* which have a creeping rhizome and simple or pinnatifid leaves not exceeding 3 cm. in length. The forms which do not range above 914 m. are all of the description:

Trichomanes punctatum Poir.

Trichomanes Krausii Hook. & Grev.

Trichomanes sphenoides Kze.

Trichomanes membranaceum L.

Trichomanes polypodioides L.

CLIMATIC CONDITIONS IN THE RAIN FOREST.—Some notion of the climatic conditions in the zone of maximum occurrence of the Hymenophyllaceae may be had from the series of records kept at Cinchona since 1871. The position of Cinchona on the leeward slope of the main ridge of the Blue Mountains, together with the exposure of the instruments in an open lawn, keeps this record from giving a full indication of the moistness of the rain forest itself. The writer judges from personal experience that the rainfall is between 20 and 30 per cent greater and the number of rainy days between 10 and 15 per cent greater in the forests than is indicated in the following figures for Cinchona:

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Year
Rainfall . . .	7.26	4.09	5.32	6.36	11.10	8.00	3.89	8.29	9.22	18.57	12.32	11.11	104.77
Ry. days . .	14.1	12.5	12.8	12.9	18.1	13.5	10.8	11.2	16.1	21.4	18.3	16.2	179.4
Humid. . .	84.1	83.1	83.9	83.4	85.2	84.8	79.6	80.4	84.4	88.9	86.0	86.3	84.1

In the course of some general work on the Blue Mountain region not yet published, the writer had occasion to expose a combined thermograph and hygrograph in a number of localities, and the record sheets figured herewith give a graphic conception of the daily march of temperature and humidity under natural forest conditions. The instrument was supported on an open framework one meter above the ground and sheltered by a canvas cover spread widely above it so as to keep off rain but permit a good circulation

of air. The sheet shown in fig. 1 was obtained in the forest at New Haven Gap during the week of April 16-22, 1906, and that

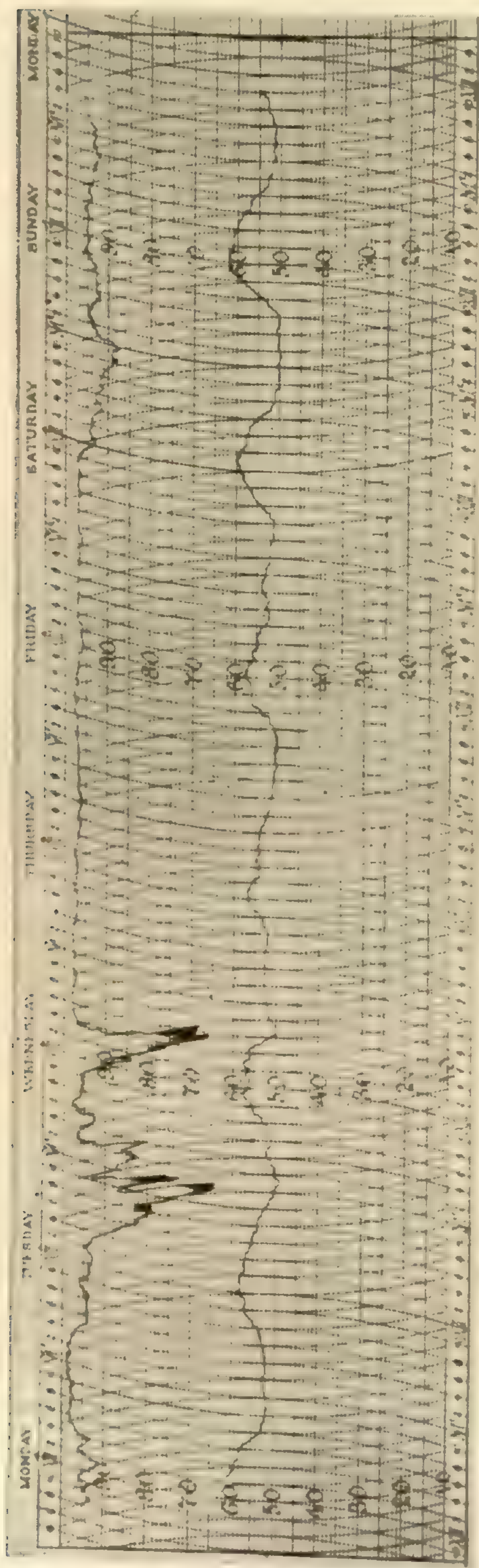


FIG. 1.—Record of temperature (the lower trace) and humidity on the floor of the rain forest at 1725 m. altitude.

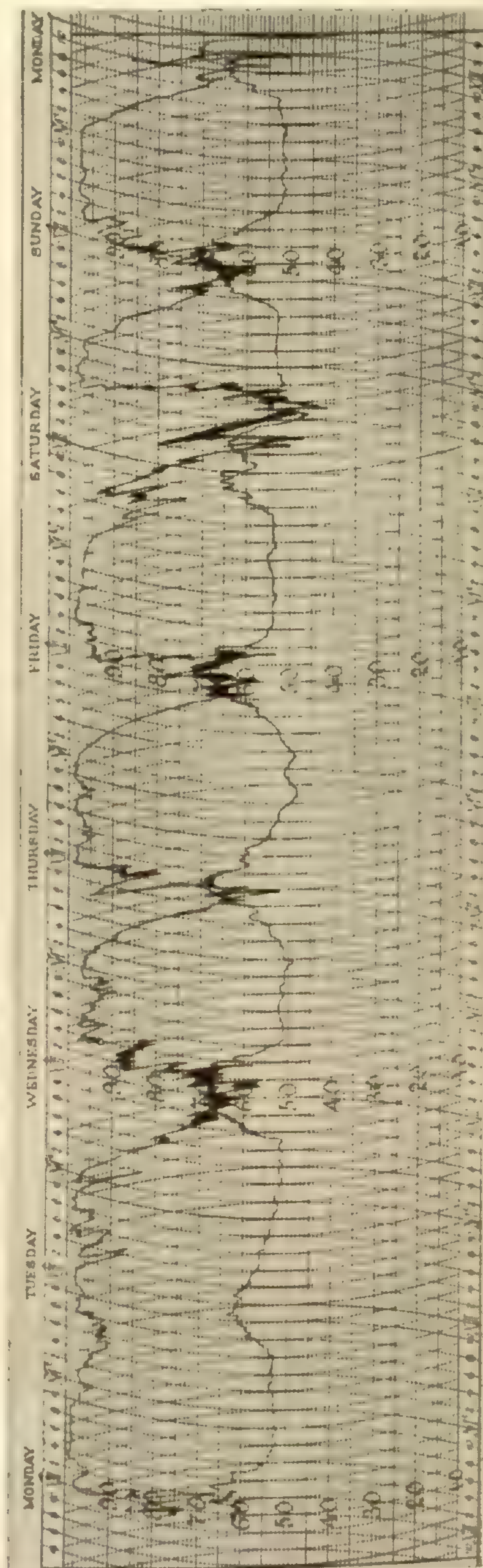


FIG. 2.—Record of temperature and humidity in a clearing in the rain forest at 1725 m. altitude.

in fig. 2 in a clearing in the forest about 200 m. distant during the preceding week. The weather of the two weeks happened to be

closely similar, and the difference in the curves of humidity brings out strikingly the degree to which the conditions on the forest floor differ from the general climatic conditions of the region. Epiphytic vegetation in the canopy of the forest is subjected to fluctuations in humidity similar to those of the clearing, together with the slightly higher range of temperatures. The high and constant humidity conditions indicated in fig. 1 are characteristic of the deep forests of ravines and lower slopes throughout the Blue Mountain region from 1200 m. to the highest peaks, while the more open forests of the upper slopes and ridges have a climate approaching more nearly that of the opening.

LOCAL DISTRIBUTION OF THE HYMENOPHYLLACEAE.—SCHIMPER⁴ has pointed out the distinctness in the character of the epiphytic vegetation near the forest floor and in the tops of the highest trees as observed by him in the forests of Trinidad and Venezuela. There the lowest epiphytes in the forest are tender hygrophilous plants which show no structural adaptations to the epiphytic habit and are often found as terrestrial plants. On the higher limbs and twigs of the largest trees are found xerophilous and succulent epiphytes possessing marked specialization in structure and in the ecology of reproduction. The Jamaican rain forest region has a highly developed erosion topography. Only in the ravines does the vegetation approach the stature and luxuriance of such lowland forests as were visited by SCHIMPER, and in them may be observed the same contrast in the character of the epiphytic vegetation. On the slopes, ridges, and peaks the forest trees are not so tall by one-half as in the ravines, and the canopy is much more open, particularly on the ridges and peaks. This results in the forests of the upper slopes being devoid of the epiphytes of the lowest levels of the ravine forest, while on the ridges and peaks the epiphytes which are characteristic of the canopy of the ravine forest may be found growing down to the forest floor. In other words, the trees of the upper slopes have the same epiphytic flora that would be found in the upper two-thirds of the trees of the ravines, while the trees of ridges and peaks have only those that are char-

⁴ SCHIMPER, A. F. W., Die epiphytische Vegetation Amerikas. Bot. Mit. aus den Trop. Heft. 1. 1888.

acteristic of the uppermost third, and the mid-height species are restricted in these habitats to the sides of prostrate trunks or fallen logs. These facts concerning the epiphytic vegetation in general are the key to the local distribution of the Hymenophyllaceae; the most important factors governing their distribution are those that have to do with the vertical differences in climate in the rain forest.

The commonest filmy ferns that are invariably rooted in the soil on the floor of the forest are *Trichomanes rigidum*, *T. radicans*, and *T. scandens*. The first of these has a short erect rootstock and its cluster of stiff leaves grows to a height of 20 cm. It is found on the floor of deep ravines or elsewhere in dense shade, and its constant wetness is well attested by the growths of epiphyllous hepatics which cover all but the youngest leaves. *Trichomanes radicans* is a climber, sometimes reaching as much as 2 m. from the ground, but only in the most moist situations. Like the foregoing species it has finely dissected leaves, the branches of which are winged with upturned leaf tissue, providing it with a ramifying system of gutters, which happen to serve well in distributing over the leaf the chance drops of water which fall from overhanging foliage.

There are a number of facultative epiphytes with erect leaves which either grow in clusters out of an erect rootstock or are spaced along a horizontal rhizome. These do not often grow in the soil itself, but are commonly found on the ground rooted in tufts of moss, on fallen logs, or on the bases of the trunks of trees. These forms are slightly tolerant of the drying off of their leaves, but they are never found over about 2 m. from the ground except in the deepest ravines. The habit of the leaves being erect, their wetting must take place from rainfall or the dripping of wet foliage; their roots, however, are very favorably situated as respects water supply. The common members of this category are: *Hymenophyllum abruptum*, *H. ciliatum*, *H. microcarpum*, *Trichomanes Hookeri*, *T. pyxidiferum*, and *T. capillaceum*. *Trichomanes capillaceum* has the most delicately cut leaves of any of the Jamaican species; and its commonest habitat is the bases of the trunks of tree ferns, where it is rooted among the coarse rhizoids of the tree fern and is

usually shaded and sprinkled by the overhanging leaves of the climbing fern *Lomaria attenuata*. *Hymenophyllum asplenoides* is quite as closely restricted to the most moist habitats as are any of the above-mentioned species, but the fact that its leaves are pendant confines its occurrence to tree trunks and rocks.

Another group of species may be characterized, which are not sharply separable from the last, but are on the whole much more



FIG. 3.—A typical colony of *Hymenophyllum sericeum*, pendant from a horizontal limb bearing mats of *Ptilidium*; one-fourth natural size.

capable of enduring desiccation and insolation. They are never found on the floor of the forest in ravines nor as low-growing epiphytes there, but are mid-height epiphytes in ravines and are found on the lowest layers of the slope forests. Their leaves are erect and glabrous, growing singly along a creeping rootstock and not exceeding 10 cm. in length in any species. These are *Hymenophyllum polyanthos*, *H. fucoides*, *H. catherinae*, *H. tunbrigense*, and *Trichomanes crispum*. *Hymenophyllum polyanthos*



FIG. 4.—A tree in the drier rain forest of the leeward slopes of the Blue Mountains, with epiphytic colonies of *Hymenophyllum sericeum* growing up to 6 m. from the ground.

is the commonest filmy fern in Jamaica, and, with the exception of the hairy forms to be mentioned, it is the most capable of resisting desiccation of any of the species. On losing water its pinnae curl downward and the midrib itself then curls, so that the whole leaf tends to close into a form resembling the circinate shape of a young leaf. *Hymenophyllum fucoides* and *H. catherinae* have also characteristic modes of curling up on becoming relatively dry. The writer has seen the rain forest on exceptionally bright days, when the humidity had fallen to 60 per cent, when every plant of these three species was curled in a marked degree. The curling is not at all in such a manner as serves to protect any part of the leaf from further desiccation.

The three pendant hairy forms *Hymenophyllum sericeum*, *H. lanatum*, and *H. hirsutum* are the most resistant to drying and insolation of any of the filmy ferns. Their pendant habit confines them to the sides or bottoms of logs and leaning trunks, and they are most flourishing just beneath large clumps of mosses and hepatics, which serve as reservoirs from which supplies of water may be secured for several days after a rain. *Hymenophyllum sericeum* is not common in the topmost limbs of trees, probably through the lack of the moss substratum, but it grows in situations where it must often be subjected to two or three hours of sunshine on clear days, and it sometimes occurs as much as 12 m. above the ground in slope forest (figs. 3, 4). As the leaves grow the old pinnae die off, so that it is not an uncommon thing to find a naked rachis 30-40 cm. long with a dozen pairs of young pinnae at the tip. There are two hairy pendant species of *Trichomanes*, *T. lucens* and *T. crinitum*, but they are not at all resistant to desiccation. They are almost confined to the under sides of rotting logs, where they are rooted in the log itself and sheltered from rain and the drip from foliage. The writer has seldom seen wet leaves in nature in either of these species, both of which have a metallic gray-green color. Their physiology has not been investigated.

Physiology

ROOT-ABSORPTION.—In order to test the ability of the various species of Hymenophyllaceae to secure by root-absorption all the

water required in a humid atmosphere, a number of individual plants or clumps of plants with undisturbed substratum were brought into the laboratory and the leaves allowed to dry off, but not to curl through too great loss of water. The plants were then placed under bell jars in which the humidity was kept above 90 per cent, and the roots wetted every day or two without wetting the leaves. It was not necessary to take any precautions against condensation of moisture on the leaves, for whenever the atmosphere in the bell jars approached saturation there was immediate condensation on the cool walls of the jar, lowering the humidity. The following data record the result of this test:

Trichomanes rigidum lost turgor in 5 days; dead in 14 days.

Trichomanes radicans remained normal for 40 days, with the chloroplasts on the lateral walls.

Hymenophyllum microcarpum remained nearly normal for 40 days, some groups of cells having become disorganized.

Hymenophyllum ciliatum remained normal for 40 days.

Trichomanes capillaceum remained normal for 40 days.

Hymenophyllum asplenoides remained normal for 40 days.

Hymenophyllum polyanthos remained normal and grew for 40 days.

Hymenophyllum sericeum remained normal and grew for 40 days.

The only form in this series incapable of maintaining its turgidity (*Trichomanes rigidum*) has already been stated to be one of the most hygrophilous, and those capable of growing under the conditions of the experiment the least hygrophilous of the Jamaican species. The extremely low water loss from surface-dry leaves in a very moist atmosphere can be met, therefore, by root-absorption and conduction in all but the most pronouncedly moisture-loving species. There are certainly no other common species which rank with *Trichomanes rigidum* in this respect; even the extremely delicate *T. capillaceum*, also requiring the most moist habitats, when kept subsequently under the conditions of this test maintained a normal condition for 35 days, at the end of which time the experiment had to be discontinued.

The conduction of root-absorbed water to the leaves is through a vascular system very poorly developed as respects the number and size of the water vessels, and the path of the water from the veins of the leaf to the transpiring cells lies through other cells, perhaps

only as many as 4 or 5 in the finely dissected forms, but as many as 10 in *Trichomanes crispum* or 25 in the simple leaves of *Trichomanes Hookeri*. In *Trichomanes rigidum* the number of walls between the vessels and the marginal cells is 6–8, but an examination of the lateral walls shows them to have a peculiar thickening, which gives the central part of each one as seen in section the appearance of having a double convex lens inserted in it (fig. 5). These ridges occur in the lateral walls throughout the leaf, so as to provide the leaf with a rigid meshwork which is calculated to strengthen it in very much the same way that a piece of wire glass is strengthened by the wire netting imbedded in it. Although at every point in the lateral walls there are areas of thin wall above and below the

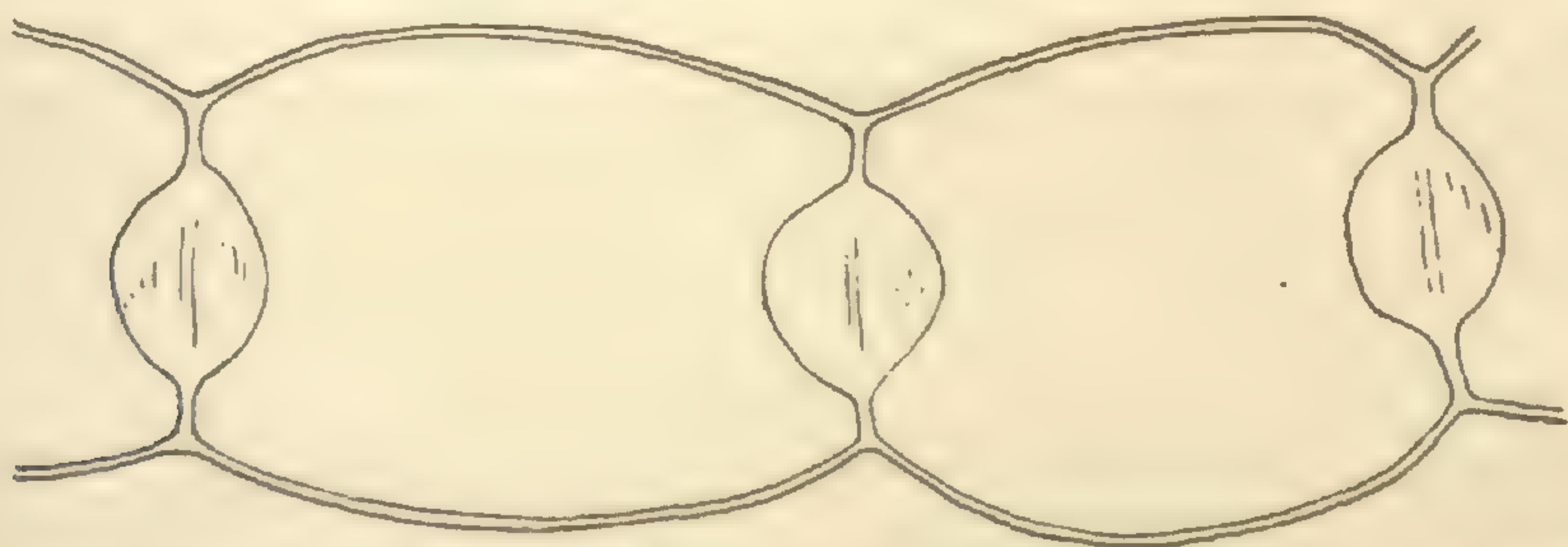


FIG. 5.—Vertical section of the leaf of *Trichomanes rigidum*, to show the mechanical thickening of the lateral walls; $\times 764$.

thickening, yet it can be readily seen that the thickenings serve to hinder the transfer of water from cell to cell, and may be accountable for the inability of this species to secure root-absorbed water quickly enough to meet even the demands of transpiration in a nearly saturated atmosphere. Although *Trichomanes capillaceum* is quite as hygrophilous a form as *T. rigidum*, it has to its advantage as respects water movement in the leaf the fact that its marginal cells are never more than 4 or 5 cells removed from the veins, and also that in its slightly thickened walls there are intercellular passages, capable of functioning as avenues for the ready transfer of water.

TRANSPIRATION.—For the measurement of transpiration in the Hymenophyllaceae the only method available is that of the potometer, which admits of having the leaf surface wet or dry. Attempts to use entire plants on the potometer were not satisfactory, and the slenderness of the petioles of most forms, together

with the smallness of the leaves in others, excluded from use all but *Trichomanes crispum*, *T. radicans*, and *T. rigidum*. Similar mechanical difficulties made it impossible to investigate the root pressure, so it is not possible to state what relation the facts ascertained by the potometer method as to the intake of water by transpiring leaves may bear to those which hold true for intact plants in a state of nature. In plants in which the transpiring surface is also capable of absorption, and in which there is no structural nor functional means by which transpiration is limited or regulated, it is to be expected that the rate will be largely a function of the conditions governing evaporation.

A single leaf of *Trichomanes crispum*, freshly cut from the plant and mounted on the potometer, was placed under a bell jar and kept wet by a drip from an opening in the top of the jar. There was no forward movement of the bubble in the potometer tube during the nine hours through which the test was run. In one of the two repetitions that were made there was a backward movement of the bubble at the rate of 1 mg. per hour during the early afternoon, suggesting a backward movement of water in the vessels due to the absorbing activity of the leaf surface. In order to compare the behavior of leaves only partially wet, the test was repeated so as to have the leaf wet at the start but without drip to keep it so. The following figures are the total losses in mg. for the intervals indicated:

11:00 A.M., leaf partly wet	
12:15 P.M., leaf just dry	73.5
1:15 P.M., leaf beginning to curl	61.0
1:16 P.M., leaf wetted again	
2:45 P.M., leaf beginning to dry off	4.0

Similar results were obtained with *Trichomanes radicans*. Neither in the dull diffuse light used in all other experimentation with the Hymenophyllaceae nor in bright diffuse light did thoroughly wet leaves show an intake of water through the petiole. A single test was made with a partially dry leaf of this species. The leaf had been mounted on the potometer since 9:00 A.M. and kept wet until evening. At 5:30 P.M. the drip was stopped and the bell jar left over the leaf during the night. At 9:00 the next morning

the leaf was partly dry, but not sufficiently so for the tips of the pinnae to have begun to curl, and the basal pinnae were still wet. The intake of water during the $15\frac{1}{2}$ hours was 39 mg.

The backward movement of the bubble in the test with *Trichomanes crispum* suggested determining the behavior of a leaf kept completely wet for several days. *Trichomanes rigidum* was used in this experiment, and in order to prevent any portion of the leaf from becoming dried the whole was submerged under a water-tight bell jar in the manner shown in fig. 6. The following figures show a continuous and uniform retreat of the potometer bubble:

		Readings	Amts. per hr.
Oct. 31,	10:50 A.M.	65.5	
Oct. 31,	2:15 P.M.	63.5	0.60
Nov. 1,	9:00 A.M.	59.5	0.24
Nov. 1,	3:00 P.M.	57.8	0.26
Nov. 1,	6:00 P.M.	57.0	0.26
Nov. 2,	9:00 A.M.	54.0	0.20
Nov. 2,	12:00 noon	53.0	0.33
Nov. 3,	10:00 A.M.	47.3	0.26
Nov. 3,	12:00 noon	46.5	0.40
Nov. 3,	3:15 P.M.	45.5	0.30
Nov. 3,	6:15 P.M.	44.5	0.33
Nov. 4,	9:00 A.M.	40.5	0.27
Nov. 4,	12:00 noon	39.5	0.33
Nov. 4,	3:00 P.M.	38.5	0.33

That the pressure of the water surrounding the leaf had to do with this retreat is scarcely probable, in view of the hourly rate at night being always less than by day. While an intake of the amount here observed would be impossible in intact plants without exudation at the roots, the experiment gives an excellent demonstration of the absorbing power of the leaves, and the greater amounts absorbed by day than by night point to an influence exerted by photosynthetic activity on the absorption rate.

The extreme slenderness of the petioles of the ferns most capable of resisting surface dryness made it impossible to experiment with them on the potometer, but the experiments on root-absorption indicate that those forms are capable of maintaining a regular transpiration rate when atmospheric conditions do not make it too rapid.

The work of POND⁵ and the more recent work of THODAY and SYKES⁶ goes to show that submerged aquatics absorb, and presumably exude, considerable quantities of water. Each of the two methods employed by POND showed absorption by the normal root system; the method of THODAY and SYKES showed an intake by cut shoots. The writer has not made any experiments with the

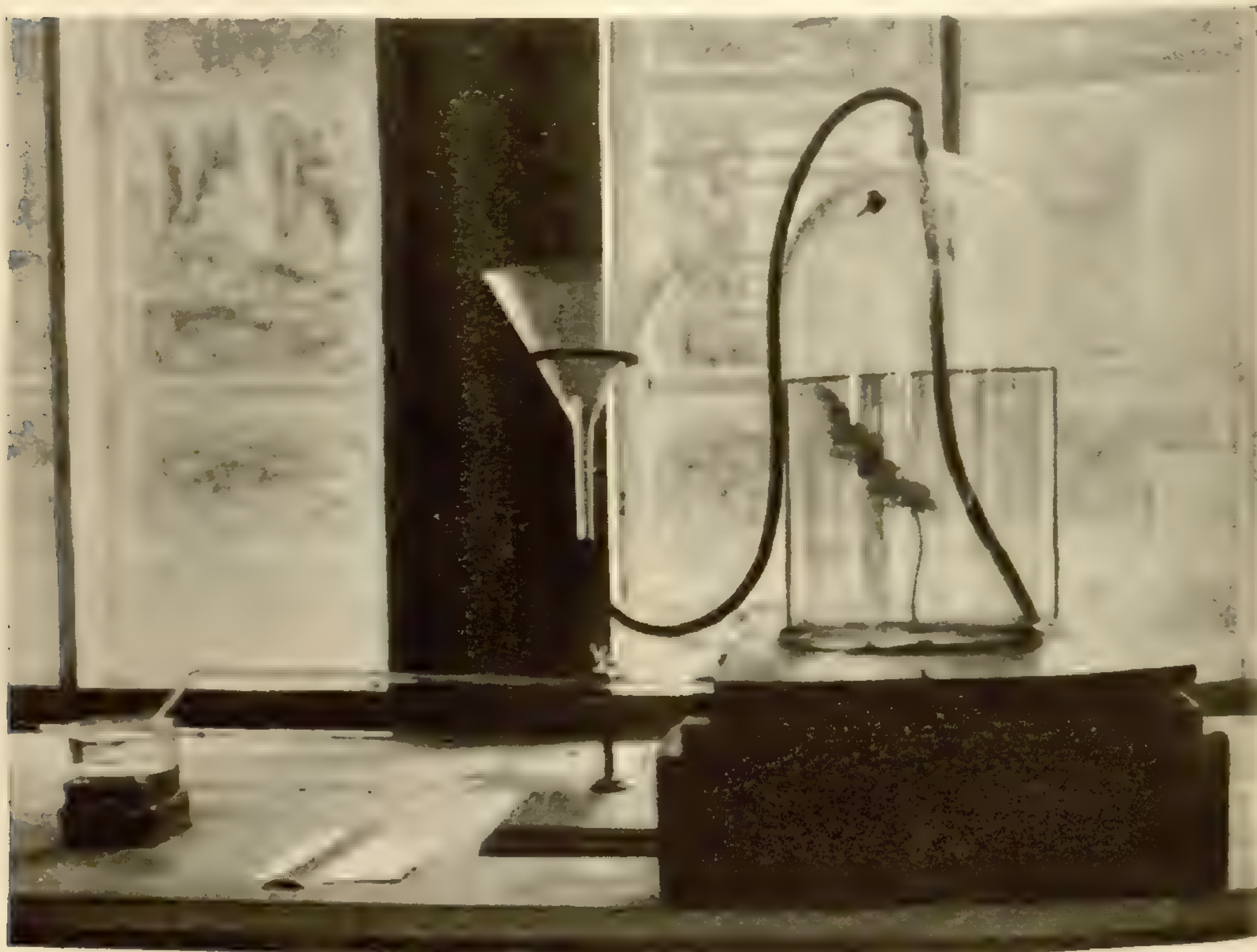


FIG. 6.—Form of apparatus used in determining the rate of leaf-absorption of water.

Hymenophyllaceae to ascertain if intact plants absorb with their uninjured root system when the leaves are wet or submerged. No evidence can be given, in other words, which is as satisfactory as that of POND for *Ranunculus aquatilis*. THODAY and SYKES showed a rapid intake of eosin solution by the cut ends of shoots of *Potamogeton*, and, if the eosin method may be trusted, their experiments go to show that the transpiration stream is quite strong even when shoots are severed from the root system. As respects

⁵ POND, RAYMOND H., The biological relation of aquatic plants to the substratum. Report U.S. Fish Comm., pp. 483-526. 1903.

⁶ THODAY, D., and SYKES M. G., Preliminary observations on the transpiration current in submerged water plants. *Annals of Botany* 23:635-637. 1909.

method, the writer's experiment with a single leaf of *Trichomanes* is comparable with those of THODAY and SYKES with severed shoots of *Potamogeton*. In spite of the violence which is done to the normal functioning of the leaves of flowering plants by removal from the plant (which will be shown below not to hold true of the filmy ferns), the writer is inclined, on the concordant evidence of the potometer experiments described, to believe that there is a standstill in the transpiration stream of a filmy fern when the leaves are wet. In exact analysis it is unthinkable that there should not be a simultaneous loss and intake of water through the leaf surface, but the backward movement of the potometer bubble shows that the absorbing activity is greater than the exudation when leaf-absorption is given play through the removal of the roots. In the intact plant, however, leaf-absorption is devoted solely to the maintenance of leaf turgidity, and the movement of root-absorbed water toward the leaves is in abeyance. When in its natural habitat, the filmy fern is now under aquatic conditions, now under those of a land plant. There may or may not be a transpiration stream in a plant according to the state of wetness of its leaves, and when the leaves are dry the ensuing root-absorption will or will not be able to meet the demands of water loss in the leaves according to the species and the humidity conditions in which it is placed. From the evidence given it appears that in nature there is now a slight transpiration stream in a given plant and now an intake of water by the leaves, accompanied by a cessation of conduction in the vessels.

TOTAL SUBMERGENCE.—A completely wet filmy fern is in a state equivalent to that of a submerged aquatic, excepting that it is under much more favorable conditions as respects the aeration of the water surrounding it. In order to determine what would be the effect of the stoppage of the transpiration stream for a considerable period, a number of plants were grown in total submergence, and in order to make these conditions as natural as possible the water was changed every four days and was aerated twice daily by injecting a fine stream of water with a large pipette. Flourishing individuals of the following species were selected, with their roots intact: *Trichomanes rigidum*, *T. radicans*, *T.*

crispum, *T. capillaceum*, *Hymenophyllum hirsutum*, *H. polyanthos*, and *H. sericeum*. At the close of 30 days of submergence these were all thriving, and the contents of the cells were of normal appearance under the microscope, save in the case of *H. sericeum*. Its leaves were blackened and the chloroplasts disorganized and lumped together. This most drought-resisting of the forms worked with (the one which is least often completely wet in nature) is therefore the only species incapable of assuming an aquatic rôle and having its transpiration stream stopped. Simultaneously with the above experiment, in which cistern water was used, an attempt was made to grow the same species in SACHS'S nutrient solution, diluted to half-strength, with fatal results to all of the cultures within the first week.

ABSORPTION OF ATMOSPHERIC MOISTURE.—In the experiment regarding root-absorption, in which plants were kept with dry leaves in a moist atmosphere, it appeared possible that the survival of the individuals used might be in part due to the absorption of atmospheric moisture by the leaves. A test was made in which 10–15 leaves were cut from each of several species, sealed at the cut ends with vaseline, and dried at 70–80 per cent humidity until all the surface water was gone and the segments had just begun to curl. These were then laid on non-absorbent paper and placed in a small chamber kept moist with wet sheets of filter paper and clumps of sphagnum. The humidity was kept continually above 95 per cent, and was usually nearer saturation. Several pieces of iron that happened to be available were placed inside, and together with the glass top to the chamber served to catch the condensation whenever the humidity approached saturation. Although an effort was thus made to prevent actual condensation of moisture on the leaves, a slight amount of it may have taken place, but if it did it is no more than might have occurred in nature, and it failed to prevent loss of weight by some of the species used. The following series of weighings was made by removing the leaves from the non-absorbent paper and placing them between large watch glasses; as the humidity of the laboratory was seldom below 75 per cent, no great error was caused by the transfer. The first weight is that of the surface-dried leaves, the following ones being

the weights on successive days while in the chamber. The chamber was accidentally opened one night, with a resulting fall in humidity that caused a loss of weight in all the leaves in it at the time, as indicated in the table by asterisks.

	Surface-dried weight	1st day	2d day	3d day	4th day	5th day	6th day	7th day
Trichomanes rigidum	1.510	1.308	1.293	1.317	1.290	1.260	1.165	1.115
Trichomanes radicans . . .	3.880	3.500	3.210	3.015*	2.787	2.550	2.600	
Hymenophyllum asplenio- oides	0.460	0.430*	0.450	0.480	0.522	0.530	0.650	
Hymenophyllum poly- anthos	0.317	0.350	0.402	0.458	0.350*	0.462		
Hymenophyllum sericeum	0.668	0.755	0.840	0.861	0.914	0.930		

Trichomanes rigidum and *T. radicans* showed themselves incapable of even so much as maintaining their original weight and became more curled each day, while the other species showed steady gains in weight and maintained a perfectly normal appearance. The fact that these species behaved differently under the same conditions, and that the gain or loss was consistently maintained in each case, together with the fact of their behavior being in accord with their habitat preferences, gives assurance of the result being indicative of their normal behavior. The more hygrophilous species, accustomed to being covered with a film of water, fail to maintain their turgidity even in the presence of a nearly saturated atmosphere, while the high epiphytes, to one of which at least constant wetness is fatal, gain appreciable quantities of water.

In order to determine whether the hygroscopic activity of the leaves of the epiphytic species was merely a physical phenomenon, several leaves of *Hymenophyllum sericeum* were killed in chromoacetic fixing fluid for 24 hours, washed for 24 hours, surface-dried, and proceeded with just as the living leaves had been. The following figures were obtained simultaneously with gains in living leaves in the moist box:

	Surf. dry wt.	1 day	2 days	3 days	4 days	5 days	6 days
Hymenophyllum sericeum	0.621	0.560	0.510	0.505	0.490	0.428	0.410

In case the chrom-acetic fluid might have altered the hygroscopic character of the cell walls, the same test was repeated with corrosive sublimate as the killing agent, and the same kind of result obtained. The leaves of *Hymenophyllum polyanthos* were also killed and carried through the moist chamber, with closely similar results.

An attempt was made to determine whether the hairy covering on the leaves of *Hymenophyllum sericeum* and related species performs any function in connection with water supply or conservation. The hairs cover both sides of the leaf densely, are multicellular, and made up of a basal stalk upon which are jointed (4-7) hairs about 0.5-1 mm. in length, diverging from each other and parallel to the surface of the leaf. Both the basal stalk and the radiating hairs are hollow and devoid of living contents. In surface-dried leaves and those commonly gathered in the field, the hairs are filled with air. Leaves which were submerged, with all of the occluded air squeezed out from among the hairs, were found after 24 hours to have their hairs filled with water. On observing the access of water to empty hairs beneath the microscope, it was seen to enter them at once and rapidly, until only a small bubble of air remained, which persisted for several hours. When leaves in which the hairs had been completely filled with water by long submergence were surface-dried with filter paper and hung in the open air at a humidity of 80 per cent, they were found at the end of 1 hour and 20 minutes to have lost approximately half the water contained in the hairs. Of the amount lost it is more than probable that as much escaped by evaporation from the hairs as became available to the leaf cells. In other leaves which had empty hairs and which were placed in a very moist atmosphere the gains in weight were not accompanied by a visible accumulation of water in the hairs. It appears, therefore, that the leaf hairs do not serve as reservoirs of water either in sufficient quantity or for a sufficient length of time to be of importance in that rôle. The coating of hairs as a whole is capable of retaining externally an amount of water equal to twice the weight of the surface-dried leaf, and under the conditions of evaporation of the rain forest this external water might be retained for 5-10 hours. The writer has placed

leaves under water without squeezing out the bubbles of air among the hairs, and found them still very imperfectly wetted up after 24 hours, and has watched dry leaves becoming wet during the commencement of rain in the forest, noticing that a heavy downpour of an hour's duration does not completely wet the leaves. It is a very uncommon thing even in the wettest weather to see leaves in the field which look saturated. The writer has no experimental evidence as to the possible rôle of the hairs in preventing water loss by the leaf cells themselves, but it is obvious that they do so to some extent, and also that they play a part in the ability of this species to withstand a greater amount of insolation than others do.

AUTONOMY OF THE LEAF AND ITS CELLS.—The extremely low degree of differentiation in the leaf tissue of the filmy ferns, and the fact that the same cells are at once capable of the functions of absorption, photosynthesis, and transpiration, seemed to indicate that the behavior of individual leaves when severed from the plant might be taken as a perfectly good criterion of their performance when *in situ*. As isolated leaves had been used in experimentation, it seemed desirable to determine their capacity for survival under the most favorable conditions. In order to do this leaves were taken from fresh plants of several species and hung in a moist chamber with wicks of cotton cord running from a pan of water so as to keep them constantly wet. The forms used were *Trichomanes rigidum*, *T. radicans*, *T. crispum*, *T. capillaceum*, *Hymenophyllum asplenoides*, *H. polyanthos*, and *H. sericeum*. At the end of 14 days all of these were in good condition, looking normal under the microscope, excepting *H. sericeum*, the inability of which to withstand submergence has already been noted. Its leaves had blackened and its chloroplasts become disorganized.

There being no reason to suppose that even portions of leaves would not survive equally well when removed from the whole leaf, a smaller series of leaf fragments was arranged, which were put in watch glasses of cistern water that was changed every other day. The only forms used were *Trichomanes capillaceum*, *T. rigidum*, and *T. crispum*, from each of which was taken a single pinna, a portion of a pinna 1 cm. long, and a portion 3 mm. long. The fragments were frequently examined under the microscope and were

allowed to run for 50 days. Up to the end of that time the pinnae and the 1 cm. pieces were normal in appearance in all three species, excepting that in *T. capillaceum* the cells had become disorganized for two or three rows back from the cut ends. The pieces 3 mm. long failed to maintain normal condition.

These tests indicate that separate leaves are capable of surviving and maintaining normal appearance, and that portions of leaves are also capable of doing so provided they are not so small that the disorganization which takes place at the cut edges leaves only two or three rows of cells along the center that might be expected to survive. So far as concerns the vegetative functioning of the plant, the leaves are quite independent of each other, and, when the leaf is completely wet, the individual cells are as independent as are those of a colonial alga.

The water by which the leaves of the Hymenophyllaceae are bathed in nature is usually rain water that has either fallen directly upon them or has dripped from foliage that has already been washed clean by frequent rainfall, and is therefore not capable of carrying any mineral salts to the plant. The water which is available to the roots, however, has usually been for some time in contact with epiphytic colonies of moss and flowering plants, and with the rotting leaves and bark always to be found beneath clumps of epiphytes, and I assume that it is rather rich in salts, including nitrates. The water which drips down over the leaves of pendant species is the same as that available to the roots of other species.

Plasmolysis with NaCl gave the following values for the osmotic strength of the sap of a few of the common species: *Trichomanes rigidum*, *T. radicans*, *T. crispum*, and *Hymenophyllum sericeum*, 0.428 N; *Hymenophyllum asplenoides* and *H. elegantissimum*, 0.514 N.

THE CHLOROPLASTS.—The chloroplasts of the filmy ferns are spherical and somewhat smaller than in most other groups of ferns. In all the Jamaican species they lie normally in a single densely packed layer next the two outside walls of the leaf cells (fig. 7). There is rarely a difference in their abundance on the two sides of the leaf.

A paleness in the coloration of the leaves of *Trichomanes radi-*

cans frequently observed in the field was found to be due to a retreat of a large proportion of the chloroplasts to the lateral walls of the cells, a performance that was afterward noticed in experiments with this and other species when isolated leaves were surface-dried and kept without access of water in a moist chamber, and also in rooted plants of *Trichomanes rigidum* which were dry as to the leaves. On the presumption that illumination was the principal factor involved in the movement of the chloroplasts, plants of several species were placed in bright diffuse light and in direct sunlight,

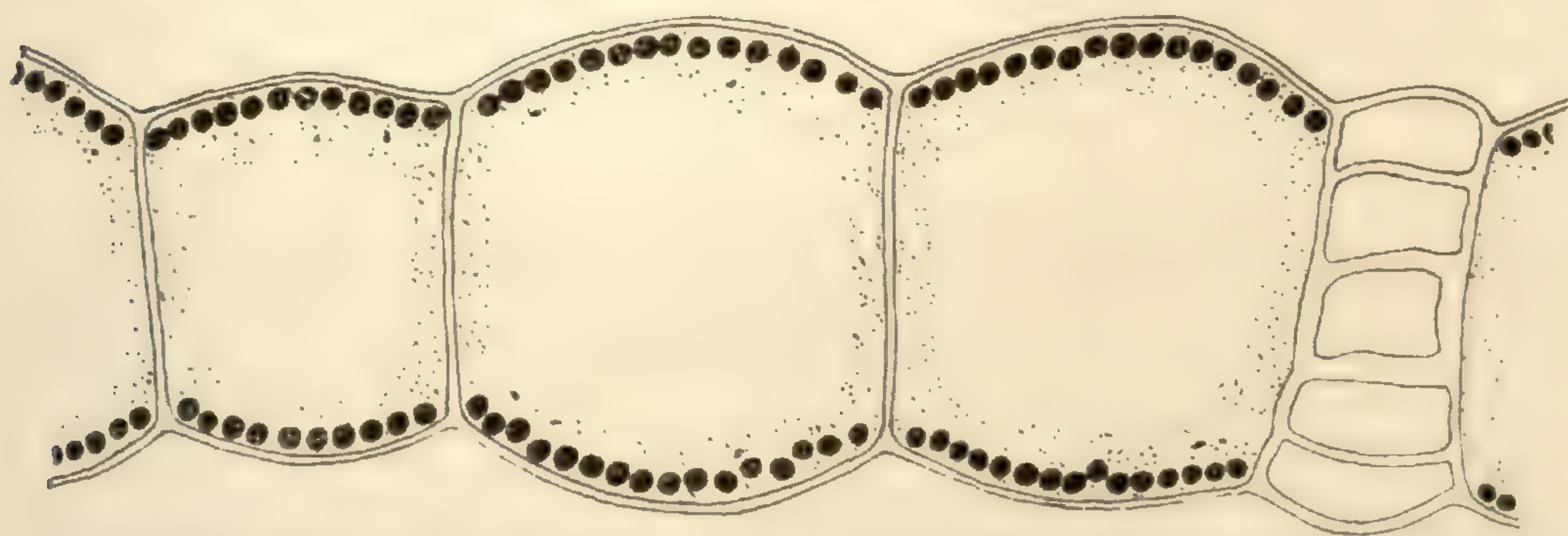


FIG. 7.—Vertical section of the leaf of *Trichomanes Hookeri*, to show the distribution of the chloroplasts and the size of the sap vacuole in a non-specialized form; X764.

the fronds being kept quite wet in the first instance by keeping the plants under a bell jar, and in the second case by submerging them. The species used were *Trichomanes radicans*, *T. crispum*, *T. rigidum*, *T. capillaceum*, *Hymenophyllum sericeum*, and *H. hirsutum*. The first of these was the only species influenced. Under bright diffuse light for 2 hours, about one-third of the chloroplasts had gone to the lateral walls, and illumination for 4 hours sent one-half of them there. The influence of full sunlight was nearly identical. When all of the above-named species were placed in total darkness for 20 hours, the chloroplasts were found in their normal positions on the outside walls.

These tests serve to indicate that intense illumination brings about a movement of the chloroplasts only in *T. radicans*. Since it is found only in heavily shaded habitats, and since species in which there is no responsive movement in strong light are found to have a portion of their chloroplasts on the lateral walls when the

surface is dry, it would appear that it is the dryness of the leaf surface rather than conditions of illumination that are responsible for the change of position of the chloroplasts.

Conclusions

The foregoing experiments have demonstrated that the filmy ferns may obtain water by any of three methods: root-absorption, leaf-absorption, and the absorption of atmospheric moisture by the leaves. By far the greatest mass of water intake is by leaf-absorption, root-absorption operating intermittently according to the wetness of the leaves. The high epiphytes are the only forms capable of availing themselves of atmospheric humidity, and the actual amounts of water thus obtained are small. The effect of a pronounced fall in humidity is to remove the water film from the leaves and to stop leaf-absorption; root-absorption is then taxed to a degree dependent on the lowness of the humidity and the duration of its lowness. Fig. 1 shows two drops in the humidity curve to below 70 per cent, neither of which lasted over 2 hrs., and it is probable that this trace, showing 4 hrs. of humidity below 70 per cent in the week, is representative of the average conditions of the floor of the rain forest.

When the surface of a leaf remains dry in a moist atmosphere, many, or even nearly all, of the chloroplasts will be found on the lateral walls of the cells. The duration of dryness necessary to bring this about varies from 3 or 4 hrs. in *Trichomanes rigidum* and other hygrophilous forms, to 8-10 hrs. in *Hymenophyllum polyanthos*. In the more hygrophilous species the removal is accompanied by a curling of the leaf, which is more a function of the humidity of the atmosphere than of surface dryness. If leaves are dried and suddenly placed in an atmosphere of 70 per cent humidity or less, the curling will take place before the movement of the chloroplasts. The movement appears to occur at times when there is no absorption of surface water taking place, but when there is a maintenance of the turgidity of the leaf by the movement into the leaf of root-absorbed water. The shifting of the chloroplasts appears, in other words, to be such as to place them opposite the walls through which the entry of water is going on.

When a gradual fall of humidity is experienced by surface-dry leaves, they assume withered shapes, and air bubbles appear in the cavities. If isolated leaves in this state are placed in a moist chamber, they will resume an appearance of turgidity within a few hours, and while the bubbles are still present in the sap. This false resumption of turgidity is therefore no more than the absorption of water vapor by the walls, and shows that the wetness of the walls rather than their distention by sap pressure is the cause of the turgidity of the leaves. The recovery of false turgidity is accompanied by considerable gains in weight, and these gains have already been shown to continue for several days. The absorption of atmospheric moisture is not great enough to replace the air bubbles in the cells when they have once appeared. Leaves of *Hymenophyllum polyanthos* with bubbles in the older cells have been kept for 5 days in a nearly saturated atmosphere without an appreciable diminution in the size or number of bubbles. The cells at the tip of the leaf and the tips of the terminal pinnae, which are richer in protoplasm, were at no time deprived of water sufficiently to have bubbles, and doubtless drew upon the supplies of water in the older cells.

The more hygrophilous species are not capable of withstanding a considerable loss of water from their sap cavities; while both *Hymenophyllum polyanthos* and *H. sericeum* have been found capable of withstanding very great losses. The extreme extent to which the lumen of the cells of *H. polyanthos* may be replaced by air is shown diagrammatically in fig. 8. The exposure of a dry leaf to sunshine for 30 min. or to very dry air (60–40 per cent) for an hour will suffice to bring about this condition. If the duration of the condition is not more than 1–3 hrs., the leaf will recover on being wet up, the chloroplasts (at first misplaced) will gradually (perhaps only after several days) resume their normal position, and the leaf will survive. A less degree of vacuolation of the leaf cells can be withstood for a longer time, but repeated attempts have shown it impossible to obtain any very exact measure of the behavior of leaves in this respect.

The physiological behavior of the Hymenophyllaceae in respect to their capacity for enduring the loss of water from the sap vacuoles

of their cells is similar to that of many xerophilous mosses, hepatics, selaginellas, and ferns. The filmy ferns are not capable of enduring as complete a removal of water as are the other archegoniates mentioned, but in view of the extremely hygrophilous character of most members of the family, it is sufficiently noteworthy that the few species which grow as high epiphytes in the Jamaican forests

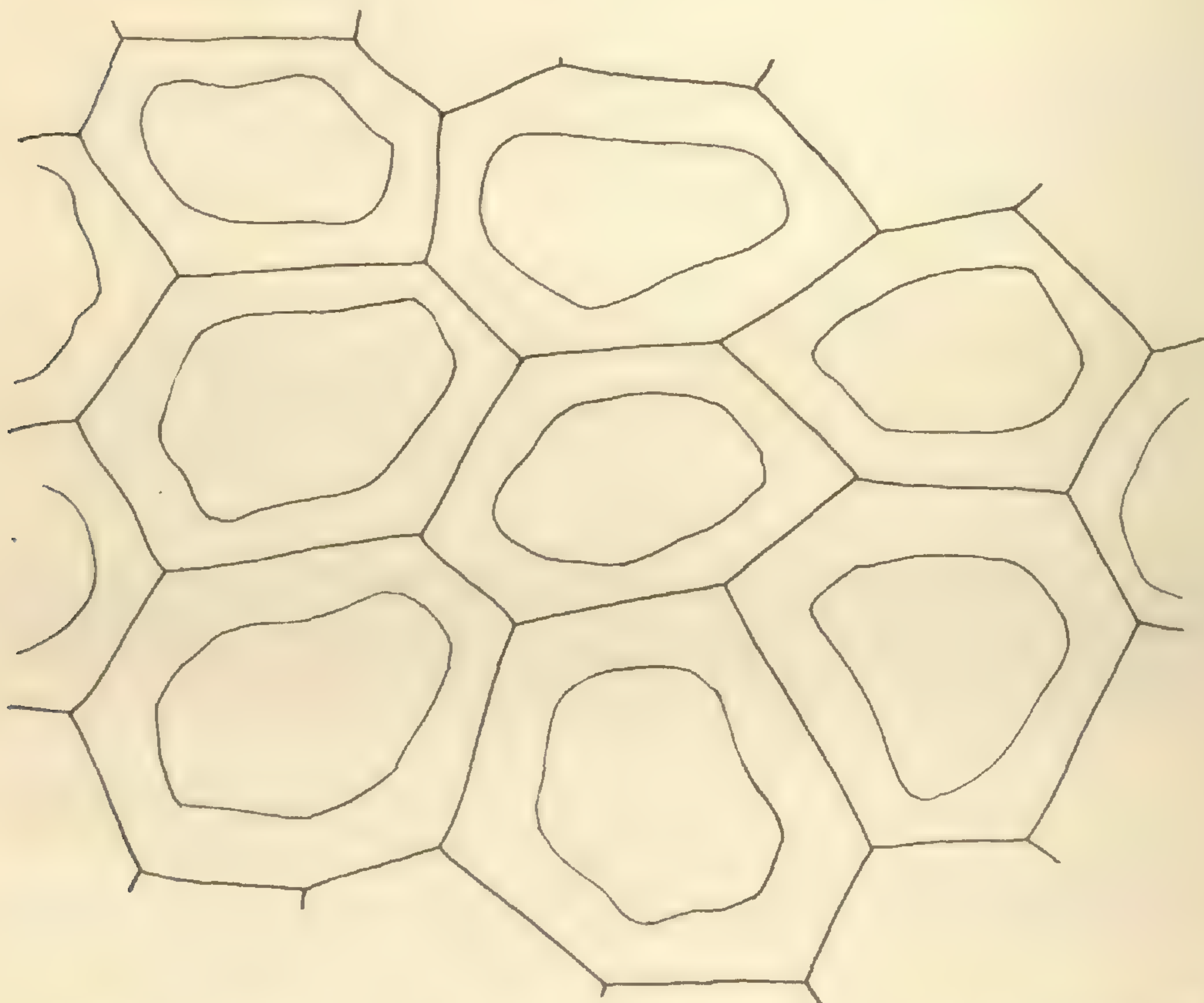


FIG. 8.—Diagram to show the maximum extent to which the sap cavities of the cells of *Hymenophyllum polyanthos* may be occupied by air bubbles in desiccated living leaves.

are capable of enduring as great water loss as they are. Whereas several families of flowering plants have contributed to the epiphytic flora of the rain forest species which are of xerophilous structure, the Hymenophyllaceae have contributed a small group of species the xerophily of which resides not at all in their structure, but in the capacity of the protoplasmic utricle to withstand the removal of the sap which is its source of water and nutrient salts.

Summary

1. The Hymenophyllaceae are most abundant in species and individuals at about 1525 m. altitude.

2. The Jamaican species differ in their relation to moisture conditions from the most pronounced hygrophily to a relative degree of drought resistance.

3. The differences of climate from floor to canopy in the rain forest determine the local distribution of the different types of Hymenophyllaceae.

4. The low water loss from surface-dry leaves in a very moist atmosphere can be met by root-absorption in all but the most hygrophilous forms.

5. The transpiration current moves when the leaves are wholly or partly surface-dry, but is at a standstill when the leaves are thoroughly wet.

6. All but the most drought-resistant epiphytic species of Hymenophyllaceae are capable of living for considerable periods as submerged aquatics.

7. The drought-resistant species are capable of absorbing atmospheric moisture when surface-dried, if kept in very moist air.

8. Continued desiccation results in the loss of the water of the sap cavity of all mature leaf cells, recovery depending on the duration of the desiccation.

9. The relatively xerophilous epiphytic Hymenophyllaceae owe their ability to resist drought to the capacity of the protoplasmic utricle of the leaf cells both to survive the replacing of the sap cavity by air and also to lose a rapidly diminishing amount of water on continued desiccation.

10. The Hymenophyllaceae (structurally and physiologically a very distinct group of ferns) have developed forms capable of growing in relatively dry situations through possession of an intracellular or functional xerophily, much less pronounced than that possessed by many mosses and selaginellas, but like it in kind.

A WAX SEAL METHOD FOR DETERMINING THE LOWER LIMIT OF AVAILABLE SOIL MOISTURE¹

LYMAN J. BRIGGS AND H. L. SHANTZ

(WITH TWO FIGURES)

All soils upon which the plant cover has wilted through lack of water will still be found to contain moisture, varying in amount from less than 1 per cent in a coarse sand to 25 per cent or more in the heaviest clay soils. It is therefore highly important in all studies of the relationship of soil moisture to plant growth to recognize clearly that a simple statement of the moisture content of the soil gives no indication whatever of the amount of water actually available to the plant. To ascertain the amount of available soil moisture, it is necessary to determine the actual water content of the soil, and in addition the minimum to which the plant can reduce the soil moisture content. The difference between these two determinations represents the soil moisture that is actually available to the plant. The minimum to which a plant can reduce the water content of a soil is dependent upon a number of variable factors, and is somewhat lower than the moisture content corresponding to the wilting point. Practically speaking, the permanent wilting of the plant marks the cessation of growth, and in accordance with previous usage has been considered in the present paper as the criterion of non-availability. In a subsequent paper, we propose to compare the minimum of available moisture, as determined by the wilting point and by the death point, and to show to what extent this determination is affected by varying conditions of temperature, humidity, and light.

The method which we have employed consists essentially (1) in the use of an impervious pot, (2) in sealing over the soil surface in the pot with wax so as to prevent all evaporation from the soil, and (3) in keeping the soil mass at approximately constant temperature. Under these conditions the water remaining in the soil at the time of wilting is non-available to the plant.

¹ Published with the permission of the Secretary of Agriculture.

Essentials in determining non-available moisture

In determining the non-available moisture content of a soil, we have found that the following precautions are necessary:

1. The soil mass should be as uniform as possible, since the non-available moisture varies with the texture of the soil, and is consequently affected by stratification or other non-uniformity of the soil mass.

2. The soil should be brought to a uniform moisture content before being placed in the pots. Otherwise, small volumes of soil may remain dry and thus introduce an error in the final moisture determinations.

3. All loss of water from the soil should be prevented except that resulting from the transpiration of the plant. Otherwise, the surface soil may dry out below the minimum limit of available moisture, before the inner soil mass has reached this limit.

4. All sudden fluctuations in temperature must be avoided. Otherwise, condensation will occur on the inner walls of the pot as the result of distillation from the soil, due to the difference of temperature. This condensed water will be absorbed by the roots in contact with the inner walls of the pot, and the moisture content of the principal soil mass may thus be reduced below the minimum of available soil moisture.

Description of the method

In working out a practical method embodying the above requirements, which have not been fully complied with in the methods heretofore described, we have adopted the following procedure:

1. The air-dried soil is sifted through a 2 mm. screen to remove gravel and to insure greater uniformity. The soil, after sifting, is thoroughly mixed, special care being taken to avoid the separation of the fine and coarse particles. Variation in the amount of gravel and coarse sand in the different pots produces irregularities in the non-available moisture determinations, due to the fact that the coarse particles add to the weight of the soil without appreciably contributing to its water-holding properties.

In certain soils, notably those deficient in lime, it is best to add a small amount of calcium carbonate to the soil before planting, to insure the growth of the seeds.

2. The proper amount of water to be added to the air-dried soil is dependent upon the soil texture, varying from 5 per cent for sand to 30 per cent for clay. The amount to be used is best determined by adding water slowly from a graduate to a small weighed portion of soil until a condition of good tilth is reached. A heavy soil can be moistened without puddling by placing it on a slab or table in a cone-shaped pile, with a large crater in the top, into which the required amount of water is slowly poured. The crater is then filled with dry soil from the sides, and the whole mass is covered to prevent evaporation, and allowed to stand over night, or preferably longer. The soil is then thoroughly mixed, during which process it is sifted through a coarse screen ($\frac{1}{4}$ inch mesh). Any pellets of soil having more than their proportionate amount of water will be removed in this way. After mixing, the moist soil should be kept in a tight receptacle until ready for use.

Impervious pots of course must be used in order to prevent the soil in contact with the pots from drying out below the minimum of available soil moisture. We have found that ordinary straight-walled drinking glasses form very satisfactory pots for this work. During the process of filling the glasses, the soil is slightly compacted by jarring the bottom of the glass against the hand. Three to five seeds are planted in each pot, about 1 cm. in depth, after which the surface is smoothed and compacted slightly. The soil surface after planting should be about 1 cm. below the edge of the glass. It is sometimes advantageous to plant seeds which have just begun to germinate; this insures a uniform stand, and avoids excessive respiration below the wax seal.

3. In sealing the pots the wax is heated slightly above the melting point, and a sufficient amount is poured into the pot to cover the soil surface about 3 mm. in depth. The pot is rocked slightly so as to bring the wax into thorough contact with the inner walls of the pot, after which the excess wax is poured off. If the wax is at the proper temperature, this will give a perfect uniform seal over the entire surface. If the seal is not perfect, the process is repeated. The wax layer should be approximately 1 mm. in thickness, and should be in close contact with the soil. If the wax does not adhere to the soil surface, the pots should be resealed, since the plants may buckle under the wax cover if it is not adherent.

In the case of monocotyledons, we have found that the wax seal can best be added immediately after planting the seeds. On germination, these plants will grow readily through the wax, which forms a perfect seal around the stems (fig. 1). With dicotyledons it is advisable to keep the pots in a moist chamber, to reduce evaporation until the seedlings appear above the ground, when the wax seal can be applied without injury to the plants.

Even in the case of dicotyledons, this wax seal is often applied at the time of planting. This prevents the soil from drying out between the time of planting and complete germination. Plants which do not raise the cotyledons above the soil surface and those with very small seeds often push through the wax without breaking the seal. Other dicotyledons push their way through the wax cover without any difficulty, although it is necessary to reseal these pots after the seedlings are all up, especially in the case of plants with large cotyledons, such as the bean, squash, cucumber, etc.

Aeration, when necessary, can readily be accomplished by making two small holes through the wax to the bottom of the pot on opposite sides. A glass tube drawn to a small opening and connected with a wash bottle is forced into one hole to supply moist air, and a similar glass tube is forced into the opposite opening and attached to an aspirator to withdraw the air from the pot. The wax forms a perfect seal around the glass tubes. In this way many pots can be aerated and the holes resealed with a hot wire in a comparatively short time.

The wax seal method is also particularly adapted to the study of transpiration, since all loss of water is avoided except through the plant tissues.

4. Serious fluctuations in temperature can be avoided by immersing the pots to within 5 mm. of the top in a tank, preferably one through which a small stream of tap water is constantly flowing.



FIG. 1.—Showing the wax seal on the surface of the soil in the glass container with wheat seedlings growing through the seal; the wax was applied immediately after planting the seeds.

In case this is not feasible, the pots can be immersed in a barrel or large tank of water, in which a constant circulation is maintained.

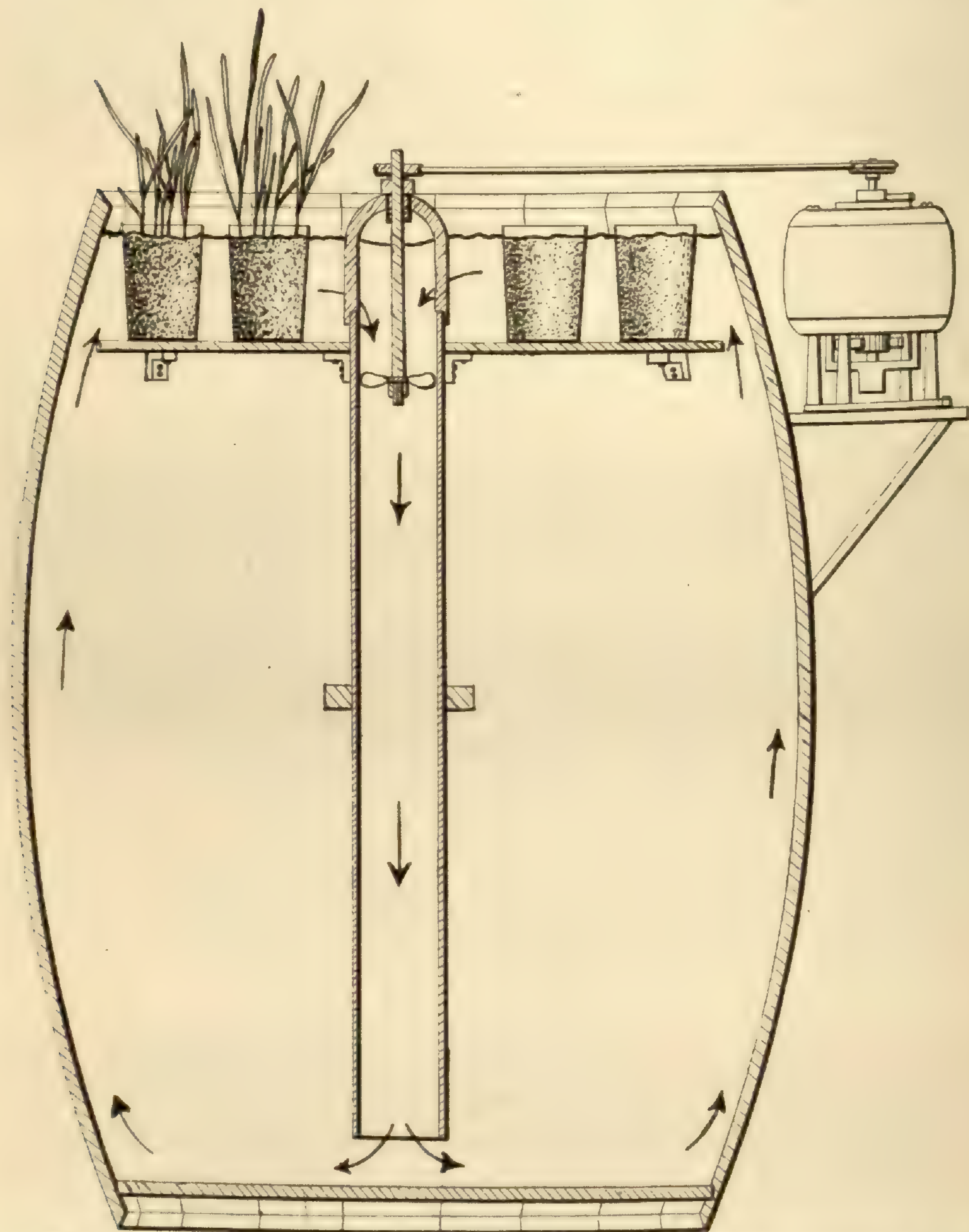


FIG. 2.—Showing tank for preventing sudden changes in the temperature of the soil used in non-available determinations; the propeller in the central tube causes a constant circulation of the water around the pots.

The most satisfactory form of stirring device that we have used consists of a small propeller in a tube (fig. 2). The upper end of the tube carries a yoke which supports the bearing of the propeller

shaft. The propeller is driven by a horizontal belt from a small vertical shaft motor mounted on a bracket at the top of the barrel. The lower end of the propeller tube extends nearly to the bottom of the barrel, while the upper end fits into the center of the solid shelf on which the pots rest. An annular space is provided between the shelf and the barrel. The operation of the stirrer causes a circulation downward through the central tube, upward along the walls of the barrel, and radially inward across the shelf and around the pots. While the temperature of even this large volume of water will vary somewhat during the day, these changes are very gradual, and are found to produce no detrimental effect. For the purpose, a simple arrangement of this kind is preferable to a more elaborate thermostat.

As soon as the plants in a pot show unmistakable signs of wilting, the water content of the soil is determined. The pot is inverted, and the soil mass removed intact by gently jarring the edge of the pot against the bench in the usual way. The lower two-thirds of the soil mass is taken for the moisture determination, since the roots do not usually develop so extensively in the upper portion. The moisture determination is based upon the loss of water taking place when the soil is dried to constant weight at 100°C. , the percentage of moisture being based upon the dry weight of the soil.

Composition of the wax seal

For sealing the pots, we have tried paraffin, petrolatum, beeswax, and tallow in various proportions. Of these, we have found a wax composed of 80 per cent paraffin (melting point 45°C.) and 20 per cent petrolatum to be most satisfactory for use at ordinary temperatures, exact proportions not being important. This mixture melts at so low a temperature and has such low heat conductivity that it can be poured into a pot around the most delicate seedling without injury. This is an important point in the case of delicate dicotyledons. On cooling, this wax adheres well to the glass and to the soil, forming a perfect seal. Other mixtures, notably those containing beeswax, show a decided tendency to separate from the glass on cooling, necessitating resealing the edges with a hot iron.

None of the substances mentioned give good results when used alone. Paraffin (45°) stretches, petrolatum creeps, and beeswax, tallow, and the higher paraffins crack. Except in the case of the soft paraffin, which stretches, the plants show no difficulty in penetrating the wax cover, even when a wax as hard as that used in making the ordinary commercial phonograph records is used as a seal.

During the winter in the greenhouse the paraffin-petrolatum mixture gives excellent results even when left in direct sunlight. However, during the warm portion of the year direct sunlight is likely to melt this wax, and in this way break the seal and cause damage to the plants, due to the wax creeping over the plant surface. The beeswax mixtures have proven best during warm weather. A mixture of 10-30 per cent beef tallow with beeswax, or of 8-12 per cent of petrolatum with beeswax, has proven an excellent material both in greenhouse and for out-of-door work.

Modelling clay has also been used to seal the pots, but it is not so easily applied as the wax, and is not suitable for use with delicate seedlings.

Experimental error

In determining the non-available moisture in a given soil, some variation will be found in the results obtained from the individual pots. This variation is probably due in part to the lack of uniformity of the soil in the different pots, but mainly to the fact that in some pots the roots are distributed through the soil mass much more uniformly than in others. When the root distribution is defective, the mean distance through which the soil moisture must move through capillary action is relatively greater. Since capillary movement is very slow in soils that are approaching their non-available moisture content, the portion of the soil not penetrated by roots would have a somewhat higher moisture content. The non-available moisture determination in the case of an imperfect root distribution would consequently be somewhat too high. On the other hand, errors arising from the distillation of water to the walls of the pot would result in giving a non-available determination below the true value.

Some uncertainty also arises in connection with the determina-

tion of the wilting point. Plants often wilt down during the day and recover during the night. The wilting of a plant in the hot part of the day is therefore no indication that moisture is not available. We have consequently considered a wilted condition in the morning as proof that the moisture content had been reduced to the point of non-availability. Check determinations were repeat-

TABLE I

INDIVIDUAL POT MEASUREMENTS OF NON-AVAILABLE MOISTURE FOR KUBANKA
WHEAT IN THREE SOIL TYPES

	Fine sand per cent	Fine sandy loam per cent	Clay loam per cent
	2.6	...	16.9
	2.1	...	16.8
	2.7	...	16.4
	2.8	9.7	16.2
	2.6	9.3	15.5
	2.7	9.9	15.7
	2.7	10.1	17.3
	2.6	9.7	16.7
	2.5	9.4	15.6
	2.6	9.6	16.0
	2.4	9.3	16.0
	2.7	9.4	16.2
	2.6	9.8	16.3
	2.5	9.3	16.3
	2.7	9.7	16.7
	2.7	9.4	16.3
Mean.....	2.59	9.66	16.3
Probable error of mean.....	±0.03	±0.05	±0.09
Probable error of single observation.....	±0.11	±0.18	±0.34

edly made by placing the pots containing wilted plants under a bell jar in nearly saturated air. These plants were unable to recover their turgidity. Since the wilting point is influenced to some extent by the temperature and humidity of the air of the plant house, these conditions should be determined and kept as uniform as possible during the growth of the plants.

The degree of accuracy which may reasonably be expected by the wax seal method is shown by the series of determinations made with Kubanka wheat shown in table I, which gives the percentage of non-available moisture found in each pot for three types of soil. The plants were grown in an ordinary plant house. The average temperature was about 70° F., and the relative humidity

about 85 per cent. The mechanical composition of the soils employed is shown in table II.

Table I shows the arithmetical mean of each series of determinations, together with the probable error of the mean and the probable error of a single observation. The term "probable error" is used in its usual mathematical sense, that is to say, in the case of the series of determinations in sand, the chances are even if the series were repeated with the same soil that the mean would lie between the values 2.56 and 2.62; and if the experiment were repeated with a single pot, the chances are even that the non-available moisture in this pot would fall between 2.48 and 2.70. The prob-

TABLE II
MECHANICAL ANALYSES OF SOIL SAMPLES USED IN THE DETERMINATIONS GIVEN IN
TABLE I*

	Fine gravel 2-1 mm.	Coarse sand 1-0.5 mm.	Medium sand 0.5- 0.25 mm.	Fine sand 0.25- 0.1 mm.	Very fine sand 0.1- 0.05 mm.	Silt 0.05- 0.005 mm.	Clay 0.005- 0 mm.
	per cent	per cent	per cent	per cent	per cent	per cent	per cent
Fine sand	0.4	9.8	17.0	50.1	14.3	4.7	3.9
Fine sandy loam .	0.1	1.5	1.2	10.2	49.6	30.2	6.9
Clay loam	0.1	2.3	2.0	6.6	13.9	52.6	22.0

* Mechanical analyses made by the Bureau of Soils.

able error of the mean is about 0.005, and that of the single observation 0.02 of the actual non-available determination in the loam and clay soils, while the corresponding probable error is about twice as great in sand. It appears, therefore, that while there is considerable variation in individual pots, the mean of a suitable series represents the non-available moisture content of a given soil with an accuracy fully comparable with the accuracy with which the soil itself can be defined through its physical properties.

Summary

All soils upon which the plant cover has wilted through lack of water will still be found to contain moisture, varying in amount from less than 1 per cent in coarse sands to 25 per cent in the heaviest clays, and even more in the peat soils. The available water in the soil at any time is represented by the difference between the actual water and the non-available portion. It is consequently

essential in any critical study of the relation of plant growth to soil moisture to be able to determine for any soil the maximum amount of non-available moisture.

In determining the non-available moisture, the permanent wilting of the plant has been taken as the criterion of non-availability. In making such determinations the following precautions are necessary:

1. The soil used should be as uniform as possible.
2. The soil should be brought to a uniform water content before being used.
3. All loss of water should be prevented except that due to the transpiration of the plant.
4. All sudden fluctuations in soil temperature should be avoided.
5. It should be definitely ascertained that the plant cannot recover turgidity without additional moisture being supplied.

The method which we have employed consists in growing the plants in a small glass pot, evaporation from the soil surface being prevented by means of a seal of wax which is melted and flowed over the soil surface. In the case of monocotyledons, this wax seal can be applied immediately after planting the seeds, and the seedlings will grow readily through the wax, forming a perfect seal around the stems. In the case of dicotyledons, the wax, which is usually a mixture of paraffin and vaseline having a low melting point and low heat conductivity, can be melted and flowed around the stems of the seedlings without injury. During growth, the pots are kept immersed in a water bath to avoid condensation of the soil moisture on the pot walls.

The probable error of the mean of the determinations from 12 pots or more does not usually exceed 0.1 per cent of actual soil moisture, which is fully comparable to the accuracy with which the soil itself can be defined through its physical properties.

The wax seal method is also particularly adapted to the study of transpiration, since all loss of water is avoided except that taking place through the plant.

THE TEMPERATURE COEFFICIENT OF THE DURATION OF LIFE OF BARLEY GRAINS

T. HARPER GOODSPEED

LOEB¹ believes that the chemical reactions underlying the development of organisms differ widely from those that bring about natural death. This author has found, for sea urchin eggs, the temperature coefficient of duration of life to lie between 500 and 1000 for a rise of temperature of 10° C., while that of development was 2.86 for a similar temperature interval. This latter figure is identical with that previously calculated by PETER² from the results obtained by HERTWIG³ in experiments upon the effect of temperature on the rate of development of frogs' eggs. MOORE,⁴ using *Tubularia crocea*, states that the temperature coefficient of life duration in this hydroid was about 1000 for a rise of temperature of 10° C., and that the average temperature coefficient for the process of regeneration was 3.4 for a 10° C. interval. The influence of temperature upon the development of plants has been given some attention; but the results, as given in the literature, with a few exceptions yield no accurate conclusions. The obvious effect upon reaction velocities of even slight variations in the temperature, when the whole temperature range employed lies well within that which is normal for the subjects investigated, is the cause assigned for the inaccuracy of the results obtained. However, the careful experiments of CLAUSEN⁵ upon the influence of temperature on the excretion of carbon dioxide by bean germs, wheat germs, and syringa buds have been widely recognized, and set a criterion of accuracy and technic for the investigations of plant physiologists along these general lines.

It was suggested to me that a temperature coefficient for the

¹ LOEB, JACQUES, Archiv. Ges. Physiol. 124:411.

² PETER, KARL, Archiv. Entw.-Mech. 20:130.

³ HERTWIG, O., Archiv. Mikr. Anat. u. Entw.-Gesch. 51:893.

⁴ MOORE, A. R., Archiv. Entw.-Mech. 29:145, 287.

⁵ CLAUSEN, Landwirtschaftliche Jahrbücher 19:893.

duration of life of seeds might yield interesting results if the determinations could be made sufficiently accurate. Experiments were accordingly begun September 1, 1910, and continued for some three months. It seemed to me that the use of barley in such an experiment would possibly yield results of the most scientific interest, since, from the observations of KIRCHHOFF⁶ to the comprehensive researches of BROWN and MORRIS⁷ and others, this member of the Gramineae has been the subject of much investigation.

The material was obtained from the American Hop and Barley Company, grown at their ranches in Butte County, California, and harvested during August 1910. The grain was given no specific name by the company, but is known in the trade as malt or brewing barley. Through the courtesy of the company, a quantity of their best grain used for exhibition purposes was at my disposal. It was characterized by them as being a trifle under the maximum weight, but uniform throughout and of the best color.

Previous to every temperature determination, the inferior palea of each barley grain was carefully removed, and 50 seeds were soaked in tap water for one hour. The material thus prepared was used within ten minutes after being removed from the water. It was judged that the removal of the outer seed coat would obviate the source of error that might otherwise be introduced through the different degrees of resistance to penetration offered by the protective coverings. By soaking previous to the experiments it was hoped that sufficient water would enter the tissues of the grain to affect a more rapid adjustment of the temperatures within and without the seed when placed in the water bath. The use of more than 50 seeds for each determination was considered to be unnecessary, inasmuch as control experiments including over 2000 seeds gave only 0.4 per cent as the percentage that would not germinate under normal conditions. This source of error may be considered negligible.

Two methods were employed for maintaining a constant temperature. In the first a double water bath heated by a Bunsen

⁶ KIRCHHOFF, SCHWEIG'S Journal 14:389. 1815.

⁷ BROWN and MORRIS, Jour. Chem. Soc. 57:458.

burner flame was used, the regulation of the temperature being made automatic by the use of a mercury thermo-regulator. A finger bowl containing 100 cc. of tap water stood upon the water bath, and the seeds, lying upon a square of loosely woven cotton cloth, were placed within it. By the use of such a container for the seeds, it was possible to remove all of the material at exactly the same moment. In the second method an electric incubator, within which stood a beaker containing 100 cc. of water, was found to give excellent results. An additional stove attachment and an electric regulator on the apparatus made it possible to maintain high and constant temperatures. When the temperature in the beaker had been kept constant at the desired point for an hour, the seeds were dropped into the water and could be taken out at the end of the time intervals almost as rapidly as in the former method. The whole temperature range given in the table below was covered according to the second method, while the effect of temperatures between 60° and 70° C. was investigated according to the first. The variations in temperature amounted to 0.2° C. for the temperatures above 60° C., and 0.3° C. for all temperatures below and including 60° C. The time during which these variations lasted, however, was relatively so short that this source of error may be disregarded.

For observing the progress of germination the seeds were placed upon moist filter paper so arranged in a finger bowl containing about 20 cc. of water that the surface of the paper was continually moist without any appreciable amount of water surrounding the seeds. In many cases the paper was perforated and the seeds, proximal end downward, were lightly pushed into the openings. A difficulty was encountered in connection with the molds *Rhizopus nigricans* and *Penicillium crustaceum*, which usually attacked the seeds on the third or fourth day. Any seeds that were evidently dead and decomposing were at once discarded as soon as the mold appeared, and any others affected but showing signs of germination were carefully watched and kept free from mold by wiping with sterilized lens paper. In all cases the material was kept at room temperature and in partial darkness.

The criterion of complete development was the appearance of the green shoot above the plumule sheath or the formation of roots from the swollen radical extremity. The normal stages observed in the germination of barley are, first, the protrusion of the calyptrogen and a rapid development of the three primary roots therefrom, and second, the appearance, at a shortly later period, of the plumule sheath, within which the leaves of the plumule are contained. The effect of all temperatures above 64°C . for the time intervals mentioned below was to inhibit in every case the normal development of the radicle. Development appeared in the plumule after intervals varying from 15 to 30 hours, and continued slowly until at the end of two days the green shoot began to show. From 2 to 3 days later adventitious roots began to take form from the basal portion of the plumule sheath, probably from the point of origin of the procambium strands that enter the scutellum, leaves, and radicle. The germination and subsequent development of certain seeds subjected to a temperature of 66°C . for 5 minutes was observed through a period of five weeks, and it was noted that after the appearance of the adventitious roots growth proceeded rapidly, and at the end of this period these plants compared favorably with those germinating normally and growing for an equal length of time.

Temperature Centigrade	Duration of life	Temperature coefficient for 1°C .
70	$1\frac{1}{2}$ -2	1.3
69	2- $2\frac{3}{4}$	1.7
68	3- 5	1.1
67	4- 5	1.2
66	5- 6	1.3
65	6- 8	1.1
64	7- 9	1.4
63	10-12	1.0
62	11-12	1.3
61	15-16	1.2
60	18-19	1.2
59	21-24	1.1
58	24-26	1.3
57	32-35	1.3
56	42-47	1.5
55	65-70	
Average temp. coefficient 1.27		

The preceding table expresses the results of some 300 separate determinations in which over 15,000 seeds were used. Each time interval was repeatedly verified, and since in some cases exactly corresponding results could not be obtained, an average was in such cases taken. The duration of life of the seeds was taken to be the time in minutes for which a given temperature must act in order to inhibit the subsequent growth of all the seeds when placed under the conditions above described.

The temperature coefficient of the duration of life of barley grains has been determined for the temperatures 55° – 70° C., inclusive, and has been found to be about 11 for a temperature interval of 10° . This is of the order of magnitude demanded by the law of VAN'T HOFF and ARRHENIUS for the temperature coefficient of a chemical reaction, but is much less than the temperature coefficient of duration of life of sea urchin eggs as determined by LOEB.

I wish to acknowledge my indebtedness to Professor W. A. SETCHELL for his many helpful suggestions and criticisms, and to A. R. MOORE, whose continued interest and assistance have made this paper possible.

UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA

BRIEFER ARTICLES

NOTES ON FUNARIA HYGROMETRICA

(WITH FIVE FIGURES)

It is usually assumed by most authors of botanical textbooks that *Funaria* is dioecious. CAMPBELL¹ says that it is "strictly dioecious." BOODLE² showed that while in general the sex organs are borne on separate plants, occasionally archegonial heads arise as branches of a main axis which is terminated by an antheridial head. HOLFERTY³ claimed that in *Mnium* the egg and ventral canal cell may sometimes be the same size. In an undetermined species of *Mnium*, COKER⁴ found two distinct eggs, with their ventral canal cells, at the base of and in direct line with the single row of neck canal cells.

While examining large quantities of *Funaria hygrometrica*, two or three well developed antheridia and the same number of quite mature archegonia were repeatedly found in the same head, which was usually conspicuous on account of its size. Also in these heads antheridia with a bulbous basal and a tapering apical region, resembling quite closely the general form of a short-necked archegonium, were not uncommon.

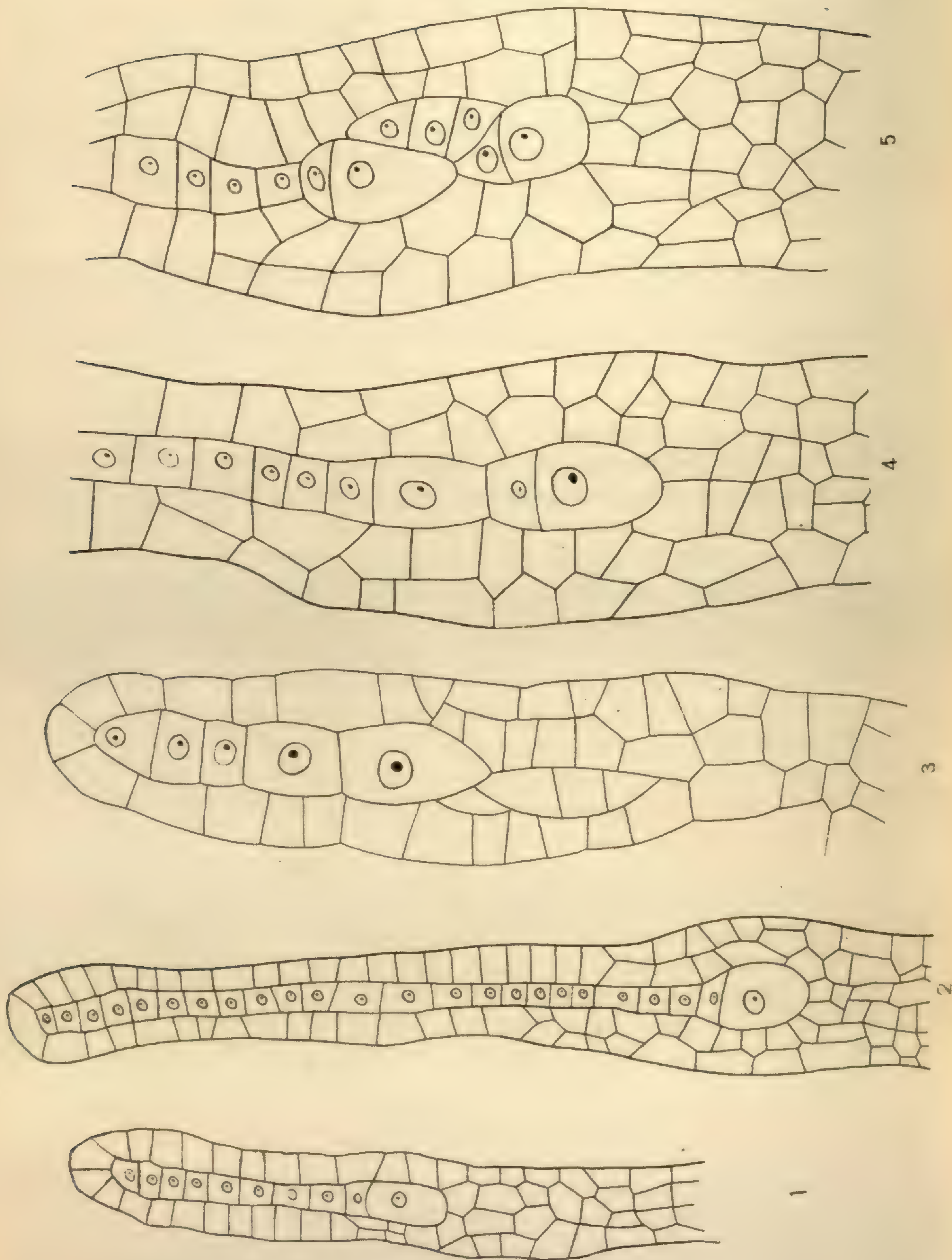
The archegonia of *Funaria* usually have 8-12 neck canal cells. An ordinary archegonium with 8 neck canal cells and the usual long stalk is shown in fig. 1. Fig. 2 shows an extremely long-necked archegonium, which had 22 neck canal cells and a relatively short stalk. This archegonium was found in a head which also bore 5 antheridia. Fig. 3 shows an archegonium in which two eggs will finally develop; the ventral canal cells have not yet been cut off. Fig. 4 illustrates the presence of two eggs and their ventral canal cells. Fig. 5 shows an archegonium having 2 eggs, each of which is definitely related to its own row of neck canal cells. The three neck canal cells belonging to the lower egg have been pushed aside by the upper egg.

¹ CAMPBELL, D. H., Mosses and Ferns, 1905. p. 195.

² BOODLE, L. A., The monoecism of *Funaria hygrometrica* Sibth. Annals of Botany 20:293-299. figs. 2. 1906.

³ HOLFERTY, G. M., The development of the archegonium of *Mnium cuspidatum*. BOT. GAZETTE 37:116-126. pls. 5, 6. 1904.

⁴ COKER, W. C., Selected notes. BOT. GAZETTE 35:135-138. 1903.



It seems that the occasional occurrence of monoecious heads and also of more than one egg in an archegonium may indicate reversions to a more primitive ancestral type.—JENNIE M. SPEER, *The University of Chicago*.

A PORTABLE, ADJUSTABLE CAMERA STAND

(WITH THREE FIGURES)

Occasion frequently arises when the scientific worker, whether in the field, at his station, in the office, or in the laboratory, needs to use the camera vertically, or at various angles between the vertical and the horizontal. The ordinary tripod does not admit of such adjustment unless special lugs are provided in the camera box. With the writer the need has often arisen for some handy method of using his camera, whereby he might photograph objects that must be kept in a horizontal position, or, in the field, where the best results require an angular view. On this account the stand shown in the accompanying photographs was devised and used with perfect success and great saving of time.

The stand is attached to any tripod by means of the standard tripod screw, and by a similar screw the camera is in turn attached to the adjustable stand as shown in fig. 2. In actual operation the tripod is set firmly with the legs spread out pretty well to give rigidity, and to allow plenty of space for the bed of the adjustable stand between any two of the tripod legs in the case of vertical work. The stand is then attached to the tripod and turned about until the bed (*b*, fig. 2) points in a direction exactly between



FIG. 1

two of the legs. The camera is then screwed in place as shown in all the illustrations. All that is then necessary, supposing the stand has been placed directly over the object to be photographed, is to adjust the camera at the proper distance from the object by sliding

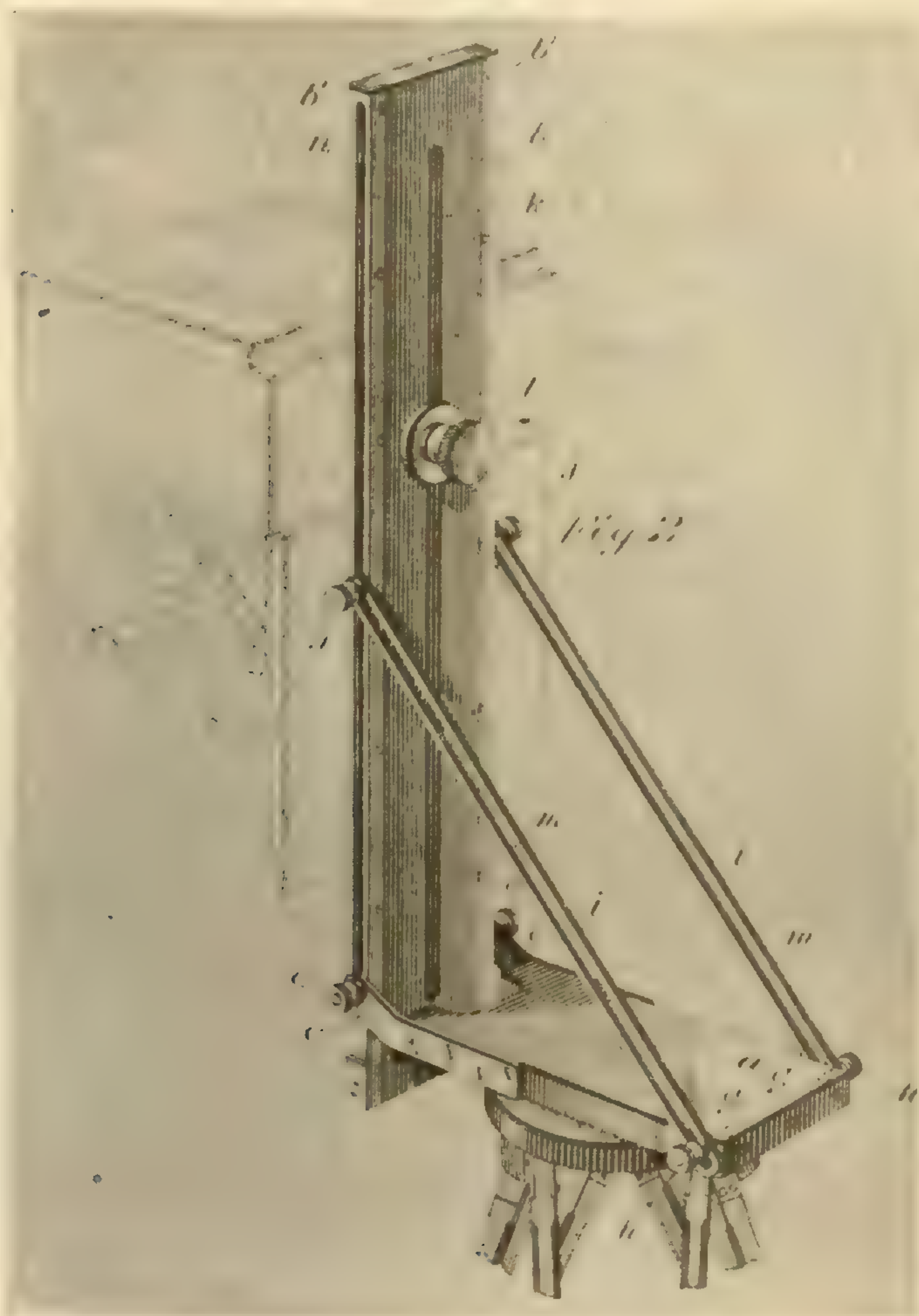


FIG. 2

it up or down the bed of the stand by means of the slot (*k*, fig. 2). The bed of the stand itself may be lowered or raised by means of the groove (*n*, fig. 2) and the binding screws (*j*, *j*, *c*, *c*). Fig. 1 shows the stand adjusted so that the camera shall be quite low, for use when objects on the ground are to be photographed on a large scale. Fig. 2 shows the stand adjusted for average vertical work; fig. 3 with the camera at an angle for photographing a plant or other object at about the same angle as it is usually viewed by a person standing near it. By reversing the camera, tall objects, such as portions of a tree, may be photographed.

The stand offers a long rigid base for quite heavy cameras and is admirably adapted for use with long-focus cameras; it may be folded compactly with the tripod or be packed in a suitcase. It is equally useful in the office and laboratory, where objects may be placed on some support, such as plate glass, to be photographed.



FIG. 3

The chief objection to any other device the writer has seen is that the tripod itself must be readjusted, always an awkward and tedious process. With this stand only the camera has to be moved to and fro on the bed to get the proper adjustment after the tripod has been set.
—HARRY B. SHAW, *Bureau of Plant Industry, Washington, D.C.*

HOMOTHALLIC CONJUGATION IN RHIZOPUS

(WITH ONE FIGURE)

A single case of homothallic conjugation in *Rhizopus nigricans* has recently been observed at the Hull Botanical Laboratory. The

hypha had curved, and suspensors had developed on opposite sides of the coil (fig. 1). The appearance of the remnants of the wall between the gametangia showed that conjugation had taken place. While investigators have disputed Dr. BLAKESLEE'S results that plus and minus strains are necessary for sexual reproduction, so far as we know the observation of conjugation between two closely approximate parts of the same hypha has not entered into the discussion. This peculiar

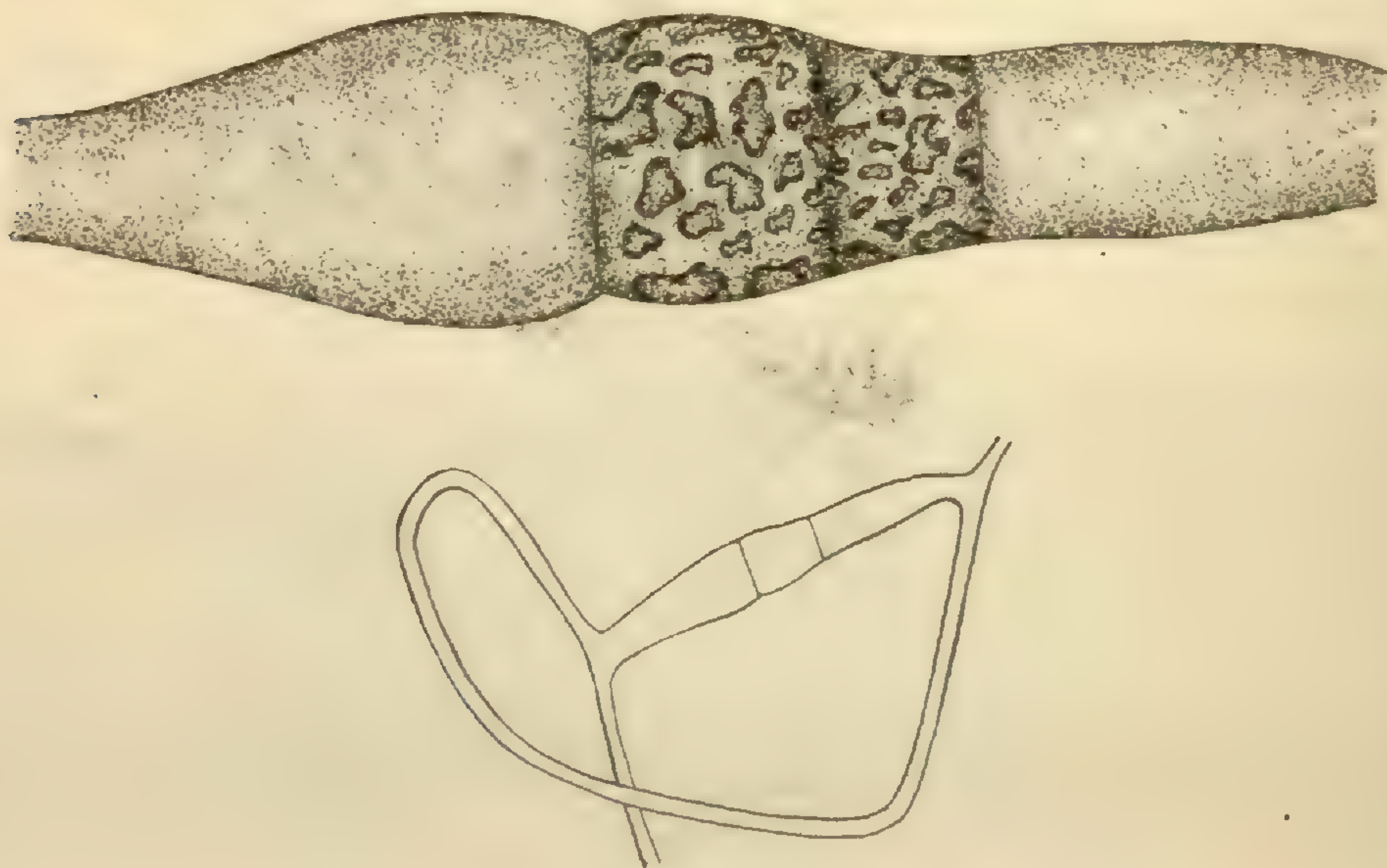


FIG. 1

mode of conjugation was accidentally found in some material grown from spores obtained from J. I. HAMAKER of Randolph-Macon Woman's College of Virginia. The culture was grown on bread moistened with a solution of grape sugar, and zygosporo-formation was unusually abundant. Dr. BLAKESLEE in his article in the BOTANICAL GAZETTE of June 1907 admits the possibility that a homothallic race may occur in a species normally heterothallic; and the case just cited substantiates that possibility.—FLORENCE A. MCCORMICK, *The University of Chicago*.

PISTILLODY OF STAMENS IN *HYPERICUM NUDIFLORUM*

A plant of *Hypericum nudiflorum* Michx. cultivated at the Arnold Arboretum and in full bloom during the first week of October, while another plant of the same species had almost mature fruits, presented a very good example of pistillody of stamens. The inflorescence and the flowers did not at the first glance show any deviation from the normal except that the regular arrangement of the stamens seemed somewhat disturbed, but a closer examination revealed the presence between the

pistil and the stamens of a number of peculiar irregularly shaped bodies representing apparently deformed carpels. These deformed carpels or pistillodes, as they may be called, were present in each flower of the whole plant, which had about eight stems, each terminated by a many-flowered cyme. The number of the pistillodes in each flower varied from three to about ten, differing in size and development. Most of them were boat-shaped, distinctly curved, and with the concave side directed toward the normal pistil; on both margins, except near the base and near the apex, they bore numerous ovules partly hidden in the concavity and partly exposed; on each side, directly below the apex, a yellow oblong spot was noticeable, which apparently represented the rudimentary anther cells, while the variously shaped apex itself usually showed a greenish color like the upper part of the style, and represented apparently the rudimentary stigma. Sometimes two of the pistillodes were more or less united at the base, and in a few cases pistillodes were divided at the apex; in one case I found one part of the divided apex representing a rudimentary anther and the other half a rudimentary stigma. Pistillodes with fertile anthers were not common; in a few cases the dilated but scarcely concave filament bore a few ovules on one side of the filament only and an anther larger than the normal, or the filament was only dilated without ovules. In some of the smaller pistillodes a few of the ovules, particularly toward the apex, were changed into greenish elongated appendages, which usually, by a peculiar bend, still preserved the anatropous character of the normal ovule. This phyllody of ovules is not at all uncommon with exposed ovules. All other parts of the flower (calyx, petals, stamens, except the few deformed ones, and pistils) were perfectly normal in all the flowers.

The teratological facts here described seemed interesting enough to be put on record, particularly as apparently no other similar case has been reported in the genus *Hypericum*. PENZIG⁵ records under *Hypericum* only cases of adventive buds, deviation from the ordinary number in the floral whorls, decrease of size in leaves, and one case of apostasis in the calyx. This tends to show that *Hypericum* has little tendency to form abnormalities, and may serve as an excuse for the publication of the present case. Specimens are preserved in the herbarium of the Arnold Arboretum.—ALFRED REHDER, *Arnold Arboretum*.

⁵ Pflanzen-Teratologie 1:308, 309.

CURRENT LITERATURE

BOOK REVIEWS

Ecology of Isle Royale

Isle Royale, Lake Superior, is a strategic point for ecological and biogeographical investigation for several reasons. It is situated in the boundary zone between two great life areas, the northeastern conifer forest region, and the eastern deciduous forest region. The isolation of the island from the mainland throughout its postglacial history has produced ideal conditions for the study of certain phases of plant and animal migration. Isolation has also resulted in unusual freedom from disturbing factors such as fire. Finally, the occurrence of certain forms far out of their ordinary range suggests opportunity for valuable floristic and faunistic investigation. The Michigan Biological Survey made a fortunate choice of a field of study when it sent the University Museum party to Isle Royale in the summer of 1905. During 1904 a similar expedition, including three of the same members, worked on the island for a few days, after spending some weeks in the Porcupine Mountains of the Northern Peninsula.¹

The 1905 expedition was under the leadership of Dr. C. C. ADAMS, now of the University of Illinois, and about half of the report² was written by him. The prime object was ecological investigation from a dynamic standpoint. In nearly every phase of the work the successional relations of the biota were emphasized. In connection with this study the forms were listed and collections made, and most of the resulting catalogues are doubtless as complete as the limited time permitted.

The first thing that strikes one in glancing over the volume is that the report is dominantly, almost exclusively, a zoological study, only 31 out of 422 pages being devoted to the vegetation. We are left absolutely without a clear idea of the vegetation of the island—its aspect and relations—in spite of the fact that the animal successions are entirely dependent upon those of the vegetation. It should be said, however, that everywhere in the discussion this necessary relation is fully recognized. The trouble is that without an adequate discussion of the vegetation as a foundation it is impossible for a

¹ An ecological survey of northern Michigan. Prepared under the direction of C. C. ADAMS. Lansing. 1906.

² ADAMS, C. C., An ecological survey of Isle Royale, Lake Superior. A report from the University of Michigan Museum published by the State Biological Survey as a part of the Report of the Geological Survey for 1908. pp. xiv+468. *figs.* 63. Lansing, Mich. 1909.

stranger to the region to gain a true conception of the interrelations of the whole biotic complex.

The report consists of two parts, including respectively ecological papers and annotated lists. Under part I we find the following: (1) Isle Royale as a biotic environment, C. C. ADAMS; (2) The ecological relations of the invertebrate fauna of Isle Royale, H. A. GLEASON; (3) The ecological distribution of the birds of Isle Royale, OTTO MCCREARY; (4) Fall migration of birds at Washington Harbor, Isle Royale, MAX M. PEET; (5) The ecological succession of birds, C. C. ADAMS; (6) The Coleoptera of Isle Royale, and their relation to the North American centers of dispersal, C. C. ADAMS. Part II includes annotated lists as follows: Notes on the vegetation of Isle Royale, and annotated lists of plants, W. P. HOLT; and various zoological lists prepared by members of the expedition and specialists.

The papers that treat directly or incidentally of the vegetation are nos. 1 and 2 of part I and HOLT's annotated list. The last, the only part directly concerned with the vegetation, comprises ten pages of ecological notes, followed by an annotated list of lichens, mosses, ferns, and seed plants. The total number of species listed is 364. That this list is very incomplete is shown by the fact that a number of species are mentioned in other parts of the report as occurring commonly, which do not appear at all in the catalogue. The very brief discussion of the vegetation that precedes the list is totally inadequate.

In the introductory paper of the report, "Isle Royale as a biotic environment" by ADAMS, there is much of interest and value to plant ecologists. The writer discusses the geologic history of the island, the climate, and the development of the habitats. The probable effect of the lake storms and surface currents in determining the composition of the flora and fauna is also treated in an interesting way.

GLEASON in his treatment of the invertebrates makes many incidental but valuable observations upon the plant successions. The brief summary with its appended generalized diagram showing the courses of the successions is the most valuable contribution to the plant ecology of the island to be found in the report.

Every ecologist, whether working with plants or animals, should read ADAMS' papers on the birds and the Coleoptera.

The report as a whole is an exceedingly valuable contribution, and Dr. ADAMS deserves great credit for carrying the work through to completion under conditions of very great difficulty. Upon such detailed studies of strategic localities will be built our future completer knowledge of biogeography. It is to be hoped that many similar expeditions may be carried out in various parts of the continent before further settlement and exploitation seriously interfere with natural conditions. It is also to be hoped that in all such studies the vegetation be given its full share of attention.—WILLIAM S. COOPER.

MINOR NOTICES

Lodgepole burn forests.—The Forest Service has recently issued a bulletin which should be of great interest to all ecologists. Dr. F. E. CLEMENTS,³ working as collaborator, has made a study of the forests of lodgepole pine in the vicinity of Long's Peak, Colorado. He finds that the lodgepole forests in that region are invariably related to forest fires, since the tree reproduces abundantly only under the conditions initiated by such events.

By a determination of the ages of the oldest plants, principally lodgepoles, which have come into the given locality since the fire, and by study of fire scars upon the trunks, he sets the date of the fire and determines the extent of country affected by it. In this way he has discovered the dates and determined the extents of many fires of the past two centuries, with considerable accuracy in the case of the recent ones, with less accuracy in the case of the less recent. Eight fires were found to have affected the region during the nineteenth century, and the areas covered by several of them overlap. There were four fires during the eighteenth century and a probable one in 1676. The accuracy with which the dates may be determined is due to the fact that abundant reproduction of lodgepole occurs the first year after the fire, and the majority of the trees are therefore even-aged to the year.

A study of the life history of the species follows, in which is found the explanation of the particular type of forest which the lodgepole pine produces. Immediate and abundant reproduction is favored by fire because (1) it causes the opening of many cones at once without damaging the seed; (2) it brings about the temporary disappearance of rodents, which ordinarily consume immense quantities of seed; (3) abundant light is provided, a necessity for reproduction and growth in this species; (4) cover competition is destroyed.

Finally, the future development and treatment of lodgepole forests are discussed. If fire is kept out, the lodgepole forest zone will be gradually narrowed and ultimately crowded out of existence by encroachment of Douglas fir from below and of Engelmann spruce and subalpine fir from above, owing to the much greater tolerance of shade which these species possess. In order to produce a new crop of lodgepole, clear cutting of the forest will be necessary, followed by thorough burning. Mere cutting without fire does not produce the requisite conditions.—WILLIAM S. COOPER.

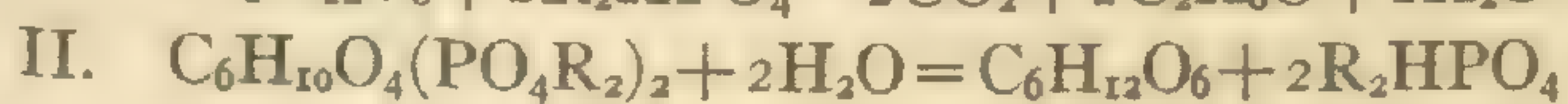
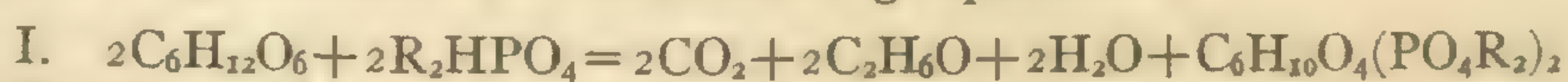
NOTES FOR STUDENTS

Alcoholic fermentation.—Important contributions to our knowledge of the fermentation of sugar have been made by HARDEN and YOUNG, and by IWANOFF, in their experiments on the action of phosphates in alcoholic fermentation. Although these investigators agree in the main, their views differ as to the details of the reactions involved in the fermentation of sugar in the presence

³ CLEMENTS, F. E., The life history of lodgepole burn forests. U.S. Dept. Agri., Forest Service Bulletin 79. pp. 56. pls. 6. fig. 1. 1909.

of phosphates. For a clearer understanding of a number of recent papers on the subject by these writers, their views may be outlined briefly here.

The view of HARDEN and YOUNG, as expressed in a number of former papers, on the manner in which the addition of phosphates to a fermenting mixture of yeast juice and sugar causes an increased evolution of carbon dioxid, is derived from the following observations. When phosphates are added to a fermenting mixture of glucose and yeast juice, the amount of carbon dioxid evolved from the fermenting mixture is greatly increased. The extra carbon dioxid is all given off during an initial period of accelerated fermentation, after which the rate of evolution decreases and continues at a uniform rate. During the initial period of fermentation, the phosphates enter into combination with the sugar in a form not precipitable by ammoniacal magnesium citrate. During the second or uniform period of fermentation, the phosphates are again set free. The carbon dioxid given off during the initial period is chemically equivalent to the amount of phosphate added. These facts are formulated in the following equations.



According to this view, the phosphate combines with the sugar to form a hexose-phosphate. This reaction gives the extra carbon dioxid evolved during the initial period after the addition of a phosphate, while the rate of the second reaction determines the steady rate of fermentation at which the simple sugars are fermented by yeast juice without the addition of phosphates.

The view of IWANOFF differs from the foregoing chiefly in the following details. The phospho-organic compound formed in a mixture of sugar, zymin, or "Hefanol" and a phosphate is a triose-phosphate and not a hexose-phosphate. The formation of the triose-phosphate is not necessarily accompanied by the evolution of carbon dioxid, because the combination takes place also when a phosphate is added to the filtrate of a sugar solution which has been fermented by zymin. Therefore, the combination may take place without the accompaniment of fermentation or the evolution of carbon dioxid.

Further evidence in support of his interpretation is given by IWANOFF in a recent paper.⁴ The main facts and conclusions of this paper may be stated briefly, without going into the experiments upon which they are based. It is found that the filtrate of a mixture of zymin and saccharose in water fermented one day is capable of combining with phosphates, but that this power of combination is lost when the filtrate is heated. The sugar which can be in part liberated from the phospho-organic compound is not fermentable by living yeast. Further, "Hefanol" washed with water will ferment the phospho-organic compound (triose-phosphate of the author), but not glucose, even after the addition of phosphate.

⁴ IWANOFF, S., Ueber die Bildung der phosphororganischen Verbindungen und ihre Rolle bei der Zymasegärung. Centralbl. Bakt. II. 24:1-12. 1909.

From these facts the following conclusions are drawn. First, the combination of sugar and phosphates is effected by a soluble enzyme to which the author gives the name "synthase." Second, if the phospho-organic compound were a hexose-compound, as maintained by HARDEN and YOUNG, fermentation by living yeast should take place after the sugar, a hexose in this case, has been liberated from the phosphate. Since such fermentation does not take place, the sugar liberated must be a triose. Third, since "Hefanol," which by washing has been freed from "synthase," will ferment triose-phosphate but not glucose, the synthesis of the triose-phosphate is a necessary intermediate step in the fermentation of sugar.

The author represents his view of the course of fermentation in three stages: (1) depolymerization of glucose, (2) synthesis of triose-phosphate by the soluble enzyme "synthase," and (3) splitting of the triose-phosphate by "alcoholase," an almost insoluble enzyme remaining in the zymin residue after washing.

In a later paper,⁵ somewhat controversial in its nature, HARDEN and YOUNG present the results of further studies bearing directly on IWANOFF's contentions. They point out that if IWANOFF's formulation of the process of fermentation is correct, the triose-phosphate of IWANOFF is an intermediate compound, the formation of which *precedes* the evolution of carbon dioxide; whereas the authors have shown that the formation of the phospho-organic compound is *accompanied* by the evolution of carbon dioxide. The case is the same whether yeast juice or zymin is used. It is further shown that the filtrate from a fermenting mixture of cane sugar and zymin, prepared after the method of IWANOFF, is still capable of producing fermentation; therefore the formation of the phospho-organic compound taking place when phosphates are added to such filtrate, is not proof that the phospho-organic compound can be formed without the accompaniment of fermentation. With regard to IWANOFF's "synthase," the authors show that the process of washing zymin employed by IWANOFF removes the soluble coenzyme of yeast juice, without which fermentation does not take place. When the boiled washings are added to the residue, the power to ferment glucose is restored. The loss of fermenting power of washed zymin is explained, therefore, by the removal of a soluble thermostable coenzyme. Since the boiled washings, if added to the residue, restore its power of fermentation, the authors contend that the reactivating power is not due to IWANOFF's "synthase," which therefore has no existence.

Other experiments bearing on this subject have been reported in another paper by HARDEN and YOUNG.⁶ Several phases of the question are taken

⁵ HARDEN, A., and YOUNG, W. J., The function of phosphates in alcoholic fermentation. *Centralbl. Bakt.* II. 26:178-184. 1910.

⁶ ——— The alcoholic ferment of yeast juice. *Proc. Roy. Soc. B* 82:321-330. 1910.

up individually. The first series of experiments relating to the ratio of carbon dioxid to sugar fermented in the presence of excess of phosphates shows that the ratio agrees with that derived from the reaction formula given by the authors, that is, $2\text{C}_6\text{H}_{12}\text{O}_6 \rightarrow 2\text{CO}_2$, for the period of accelerated fermentation that follows the addition of phosphates to a fermenting mixture.

The question as to the necessity of phosphates for alcoholic fermentation is also taken up. While it has never been conclusively shown that alcoholic fermentation cannot take place in the absence of phosphates, the experiments here given furnish strong evidence in favor of the view that phosphates are necessary for alcoholic fermentation. The authors reduced the quantity of phosphates in fermenting mixtures to a minimum, and found that the addition of very small quantities of phosphates to such mixtures increased the evolution of carbon dioxid as much as 700 per cent of the original amount; while if no precaution is taken to remove the phosphates from the mixture at first, further addition of phosphates gives an increase of only 10-150 per cent of the original. The relatively large increase in fermentation due to the addition of small quantities of phosphates is regarded as strong evidence that phosphates are necessary in fermentation.

It is further shown that the hexose-phosphate when hydrolyzed by the enzymes of yeast juice yields a sugar which is fermented by living yeast, a result which is opposed to the conclusion of IWANOFF mentioned above. The sugar thus obtained gives the reactions of fructose, although the possibility that other hexoses may be present is not excluded.

Putting the facts thus far gained into the shape of a tentative theory, HARDEN and YOUNG suggest that two molecules of hexose may be decomposed into smaller groups, two of which go to form alcohol and carbon dioxid. The other two residues are synthesized into a new chain of six carbon atoms, which forms the carbohydrate part of the hexose-phosphate.

Papers taking up the question of fermentation from a different viewpoint have been published by KOHL and by KUSSEROW. KOHL's⁷ work relates chiefly to the part played by the enzymes in the different steps of fermentation. As far as the steps by which sugar is transformed into alcohol are concerned, he adheres to the original view of BUCHNER that lactic acid is an intermediate product. BUCHNER attributes the first step in this process to the action of an enzyme which he called zymase, and which is not easily extracted from the cells by the usual solvents for enzymes. KOHL finds that none of the enzymes extracted from yeast by glycerin or water are capable of transforming lactic acid into alcohol and carbon dioxid. It is therefore this step, he reasons, and not the changing of sugar into lactic acid, which must be attributed to the action of zymase. This leaves the splitting of lactic acid into alcohol and carbon dioxid to be accomplished by some of the soluble enzymes of the yeast

⁷ KOHL, F. G., Ueber das Wesen der Alkoholgärung. Beih. Bot. Centralbl. I. 25:115-126. 1910.

extract. It is here that the author finds a function for catalase. The extract is rich in catalase, and since no other function for this enzyme is known, he makes it the active agent in the first step of fermentation according to the scheme. Nor is this view reached without apparent experimental evidence. Extracts of yeast rich in catalase were allowed to act for various lengths of time on 10 per cent glucose solutions. The solutions were found to contain lactic acid, which was identified by its zinc and calcium salts and by other tests. Unfortunately the experiments are not entirely convincing, since the only precaution to insure sterility was the addition of thymol to the flasks. It is not recorded that cultures were made from the flasks at the end of the experiments to demonstrate their sterility. The finding of oxalic acid in the flasks would seem to add to the doubtfulness of the experiments.

KUSSEROW,⁸ believing that no description of the mechanism of fermentation has been given, propounds a new theory of alcoholic fermentation. This theory is that the demand of the yeast cell for oxygen results in the reduction of glucose to sorbite, a molecule of water being involved in the reaction. The sorbite breaks up directly into alcohol, carbon dioxide, and hydrogen. The hydrogen reduces a further molecule of glucose, and so the process goes on. The view is scarcely supported by evidence, nor would the dearth of theories alone seem to warrant it, for several have been proposed.—H. HASSELBRING.

Vegetative reproduction in *Metzgeria*.—EVANS⁹ has described the gemmae of 12 species of *Metzgeria*. They fall into three groups, depending upon their position on the thallus. The first group (5 spp.) has the gemmae marginal; the second (6 spp.) has them on the antical surface of the wings; and in the third group (1 sp.) they are indefinite in position. When a gemma is to be produced, a marginal cell projects beyond its neighbors and its outer wall is ruptured. The protruding protoplast is not naked, however, but is covered by a thick layer of transparent gelatinous substance, which EVANS thinks is a modification of the inner portion of the original wall. Upon the inner surface of this gelatinous substance a very thin new wall soon appears. The projecting cell divides by a periclinal wall; the outer of these two cells is considered to be the mother cell of the gemma. A second wall meets the first, obliquely cutting off a wedge-shaped apical cell, which proceeds to cut off segments right and left. The original gelatinous substance becomes stretched by the growth of the gemma until it finally disappears. The gemma is separated from the plant by the splitting of the original periclinal wall. Along the margin of the young gemma hooked hairs appear. As it becomes older, new hairs appear, which function as rhizoids. The young gemma shows no sign of dorsiventrality.

⁸ KUSSEROW, R., Centralbl. Bakt. II. 26:184-187. 1910.

⁹ EVANS, ALEXANDER W., Vegetative reproduction in *Metzgeria*. Annals of Botany 24:272-303. figs. 16. 1910.

EVANS thinks that a vigorous apical cell exercises an inhibitory action on the production of gemmae, and that when the apical cell is suppressed, or its activity lessened, gemmae are able to form. He says:

Just why the normal activities of the apical region are lessened in these cases and finally brought to an end, is by no means clear. In some instances the result is perhaps due to poor nutrition, bringing about an enfeeblement of the whole plant; but this cannot be the effective cause in all cases, because a limitation of growth often takes place in plants which are robust. Under these circumstances the plant is probably able to control the apical growth, perhaps by diverting the currents of food to other regions. Apparently something of the same sort takes place in such species as *M. dichotoma*, where the growth of the gemmiparous branch continues for an indefinite period. The power of the plant to regulate the distribution of the nutritive materials, and thus to weaken or destroy the inhibitory influence exerted by the apical region upon the cells capable of producing gemmae, may be considered a specific character.

It seems possible that the production of gemmae may rather be due to the influence of some external factor than to an internal self-regulating mechanism; and it is possible by experiment to determine what this factor may be.—
W. J. G. LAND.

Presentation time.—RUTGERS,¹⁰ working in WENT's laboratory at Utrecht, has studied the relation of temperature to geotropic presentation time in the etiolated seedlings of *Avena*. He believes that VAN'T HOFF's law of speed of reaction for temperature holds from 5° to 30° C. with a coefficient of about 2.6 for every rise of 10°. From 0° to 10° the coefficient is 6.8. RUTGERS attributes this high coefficient to the effect of low temperature on growth. From 25° to 35° the coefficient is 0.93, and for higher temperatures still lower. The time of previous warming (varying 1 to 24 hours) has no effect up to 25°; but at 30° its effect is marked. At the latter temperature one hour's warming gives a presentation time of 3.5 min.; while 12 to 24 hours gives 1.66 minutes. These results do not agree with those of BACH.¹¹ It is certainly interesting, if true, that this chemical law applies to this supposedly complex process of perception as BLACKMAN¹² has shown it to apply in photosynthesis, and KUYPER¹³ in respiration, and various other workers in other processes.

Serious criticism can be offered against RUTGERS' methods and his discussion of literature. So far as his description of methods tells, he seems to

¹⁰ RUTGERS, A. A. L., The influence of temperature on the presentation time in geotropism. English reprint from the Proc. Konink. Akad. Wetensch. Amsterdam. Oct. 29, 1910.

¹¹ Bach, H., Ueber die Abhängigkeit der geotropischen Präsentation und Reaktionszeit von verschiedenen Aussenbedingungen. Jahrb. Wiss. Bot. 44:57-123. 1907.

¹² BLACKMAN, F. F., Optima and limiting factors. Annals of Botany 19:281-295. 1905.

¹³ BOT. GAZETTE 50:233-234. 1910.

have depended upon the unaided eye to detect reaction, and the work was done without the use of a clinostat. Methods of such crudeness must give questionable data. He states that BACH's results are not suited to test VAN'T HOFF's law, but so far as they give data they indicate a coefficient of 3.75. In contrast to this statement it should be mentioned that BACH determined the presentation time in the epicotyl of *Vicia Faba* for every two-degree change from 14° to 34° . This was done by accurate methods, and one must conclude that Bach's figures are good for testing the application of the VAN'T HOFF law between 14° and 34° . The following are the coefficients figured from BACH's table: 14° – 24° , 3.88; 16° – 26° , 4.61; 18° – 28° , 4.54; 20° – 30° , 3.80; 22° – 32° , 2.00; 24° – 34° , 1.59. As is seen here, the coefficient is rather variable.—WILLIAM CROCKER.

Anatomy of Welwitschia.—Miss SYKES¹⁴ has investigated a large number of seedlings and young plants of *Welwitschia*, placed at her disposal by Professor PEARSON. The mature plant is aptly spoken of as an "adult seedling," since the main axis consists of root and much enlarged hypocotyl. Two ridges are developed by rapidly dividing parenchyma, the inner one bearing the strobiliferous axes. Each cotyledon is supplied by a pair of collateral bundles, which unite to form one pole of the diarch root, the transition being remarkably slow, probably on account of the great length of the hypocotyl. The four cotyledonary bundles are joined by the bundles from the buds, ridges, and leaves, this association of bundles forming four concentric groups, so that there is at no time any real stem structure. In the character of four cotyledonary bundles connected with a diarch root, *Welwitschia* is associated with *Araucaria* and *Podocarpus*, and also in the details of the transition. The small amount of primary vascular tissue is a remarkable feature, being limited to the root poles, the four cotyledonary bundles, and the four connecting hypocotyledonary bundles. In the base of the cotyledon, centripetal xylem is developed in connection with the two bundles, and of course the bundles traversing the hypocotyl become exarch.

The retention of the seedling characters in the adult plant makes a comparison impossible with the stem structure of other groups; and if the vascular structure of seedlings depends to a large extent upon "habitat and environment," as the author considers probable, a seedling comparison cannot be significant in indicating relationships. The result of the study, therefore, has been to uncover some interesting facts in reference to the anatomy of *Welwitschia*, rather than to uncover some much needed suggestion as to relationship.—J. M. C.

¹⁴ SYKES, M. G., The anatomy of *Welwitschia mirabilis* in the seedling and adult states. Trans. Linn. Soc. London II. Bot. 7:327–354. pls. 34, 35. figs. 5. 1910.



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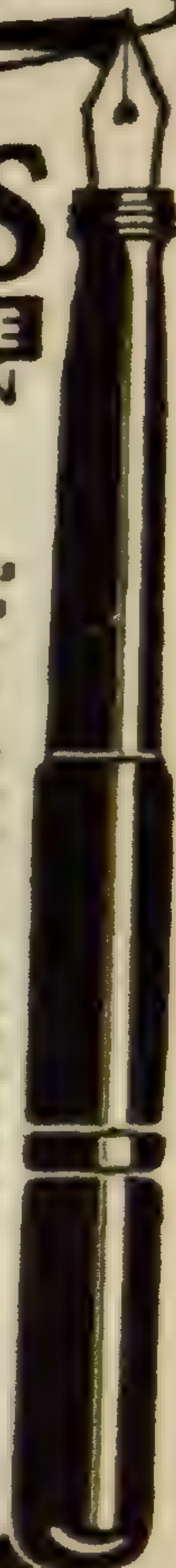
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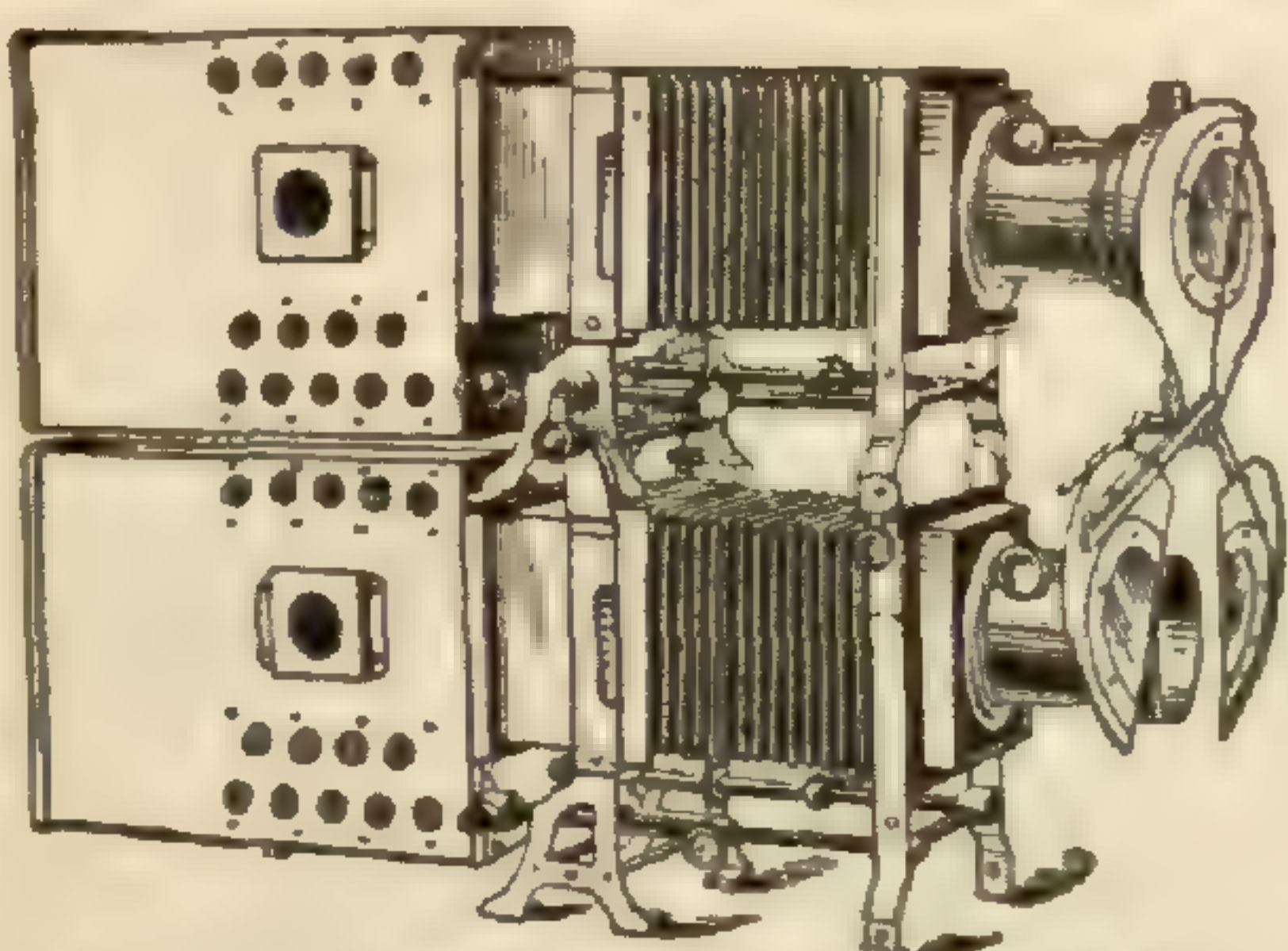
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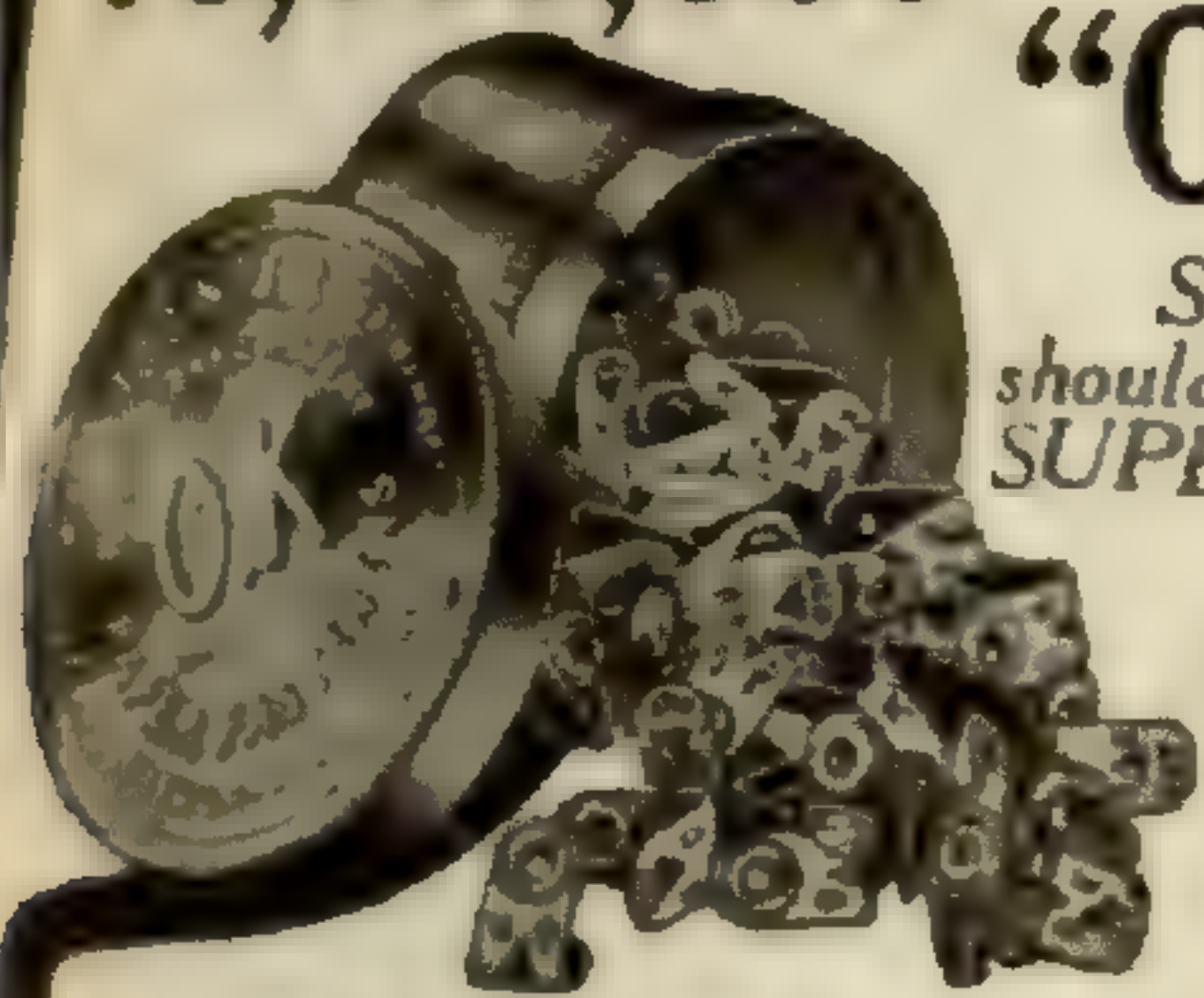
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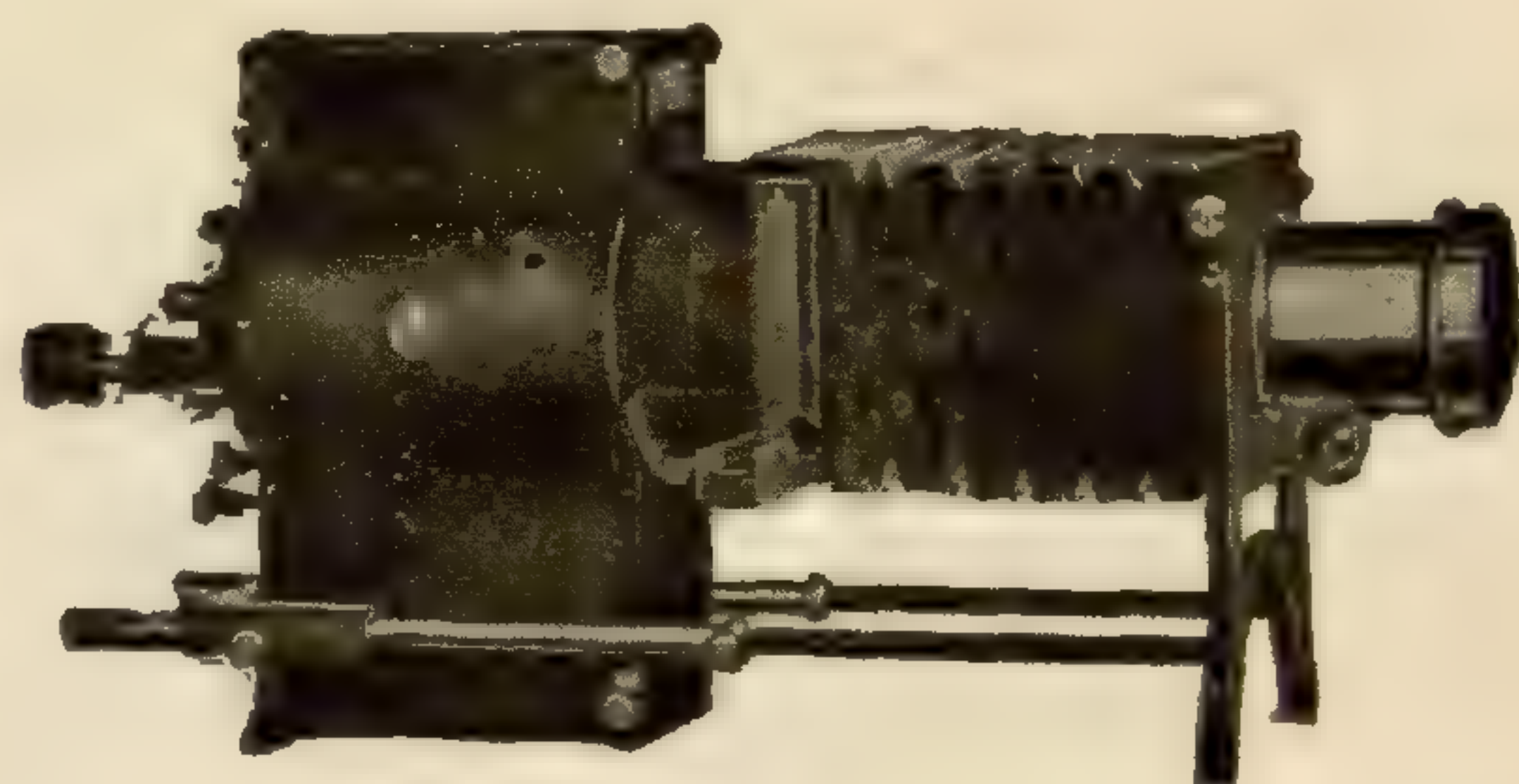
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THE
BOTANICAL GAZETTE

APRIL 1911

ALTERATIONS IN HEREDITY INDUCED BY OVARIAL
TREATMENTS

D. T. MACDOUGAL

(WITH PLATES XIV-XVI AND THREE FIGURES)

During the course of an extended series of experimental cultures of the mutants of the *oenotheras* and of a large number of other evening primroses native to America, the author conceived the idea early in 1905 that agencies of any kind which might affect the processes of the protoplasts concerned directly in the development of the embryo sac and the differentiation of the egg, and which inhibited or altered the reaction velocities of any process, whether catalytic or otherwise, might cause some alteration in the characters transmitted to the progeny arising from fertilizations into which had entered elements affected in this way.

Brief announcements of the progress of the investigation have been made from time to time, as indicated by the appended bibliography, but it has been deemed advisable to present a résumé of the entire subject, which should include a description of the technique and character of the plants employed, together with the results of the culture of the affected species through a number of generations. It may as well be stated in advance that the earlier conclusions, that the sum of hereditary characters in pedigreed lines of plants may be altered by solutions applied to the ovaries in the stage immediately preceding fertilization, are confirmed by the extended work on the matter, and that one of the earliest derivatives secured in this manner has been carried to the fifth generation without showing indications of returning to the parental type.

The original purpose was to test the matter of localization of the supposed alterations by which discontinuous variations occur in hereditary lines, a matter to which attention was directed by the suggestion of DEVRIES that mutations as exemplified by the derivatives of the *oenotheras* were consequent upon changes in the germ-plasm ensuing previous to the reduction divisions, and, if such localization were established, it was hoped that new mutations might be induced experimentally by controlled conditions or reagents.

As has been pointed out recently, CHARLES DARWIN had attempted to induce alterations in leaves by the injection of reagents which might have acted after the manner of the substances to which galls are due, but this effort was unknown to me, and it may be stated that no results of any kind were secured by him (6).

The announcement of the preliminary results to be described here brought out the information that various workers had placed the bases of excised inflorescences and branches in solutions in the effort to cause embryogenic alterations, and also that specialized water cultures had been used, but without result.

The initial tests were so planned as to include the introduction of solutions into the ovary at a time when pollen and egg were in the stage immediately preceding fertilization. Two plants were chosen for the first trial: *Oenothera biennis*, the form known to American botanists as growing wild under that name; and *Raimannia odorata*, native to Patagonia, and now distributed about the world. Pure-bred material of both species, which had been guarded from possible intercrossing since its introduction into the cultures, was available. Thousands of individuals of many generations of both plants had been cultivated, and in no single instance has anything beyond the well known forms of fluctuating variability been shown, except when diseased plants were encountered. Better authenticated material would be difficult to procure, although, as was proven later, the mechanical conditions offered by the reproductive apparatus of these plants were of such character as not to facilitate the treatment.

It was realized very quickly, however, that the use of the

methods might secure some evidence of value in its bearing upon the influence of environic factors upon germ and soma and their inheritance. This aspect of the matter has taken on an increasing importance, and a score of workers are now busily engaged in experimental inquiries by various methods for the purpose of securing evidence on this subject.

An announcement had been made earlier that *O. biennis* was in a state of mutation, but the cultivation of a second generation demonstrated that the changes under observation were due to a fungal infection (1).

The first series of reagents used were selected for the reason that they might withdraw water from the protoplasts or, by permeating the membranes, exercise a stimulative or inhibitive action upon some of the features of cell action. A 10 per cent sugar solution, solutions of zinc sulphate in distilled water varying from 1 to 10,000, and calcium nitrate 1-1000, constituted the first lot of reagents. These compounds were injected into the ovaries of the plants named during the forenoon of the day at the close of which pollinations would take place, and within 24 hours of fertilization. Every precaution was taken to prevent intercrossing by guarding the inflorescences both before and after the treatments.

A common hypodermic syringe was used, and no more than a portion of a minute drop remained within the densely packed structures of these ovaries, although other plants have since been operated upon which were capable of receiving a large fraction of a cc. of the reagent. With the refinement of technic, operations are now performed with syringes in which a plunger of ground glass is ground into the barrel of a hard glass syringe, to which are attachable needles of 14k gold, by a friction tip which permits thorough cleaning. Solutions are made up in non-sol glass and kept in flasks of the same material.

In the case of the evening primroses, the tip of the needle was thrust into the ovary in a line at an acute angle with its main axis, and as a gentle pressure was applied to the plunger, the needle was gradually withdrawn. Examinations disclosed the fact that many of the ovarial structures were destroyed, the larger number

were totally unaffected, while the reagent would come into contact with a good number in such manner that it might or might not penetrate to the egg apparatus. The shock of the operation is sufficient to cause the entire ovary to be cast off in many species, and for these the method was devised later of using vapors and gases, such as bromine. The surviving ovaries were allowed to ripen in the usual manner, and the seeds duly sowed in pans of fine soil which had been sterilized in an autoclave for several hours. Singularly gratifying results were obtained from these first two plants.

The first experimental test was made with *Raimannia*. Sixteen seedlings were secured, some from ovaries treated with sugar solution, others from ovaries injected with zinc sulphate, and others with calcium nitrate, which were identical in their general characters, being, first of all, annuals in contrast with the biannuality of the parent. This entailed, of course, the continuous formation of elongated internodes from the start, the development of rosettes being due to a stage in stem formation in which the internodes are not separable by external measurements. The cycle of stem formation was therefore a simple curve, starting with a minimum for the seedling, waxing to a maximum, then decreasing with the formation of flowers in the terminal portions, in contrast with the parent, in which the curve is nearly flat for the first season, coming to zero at its end, then rising and falling as in the derivative.

Another feature no less striking was that of the glabrosity of the derivatives, the villous and ciliary hairs of the parent being wholly lacking, no trichomes whatever being formed, these plants being the only evening primroses lacking epidermal extrusions. A number of the second generation were grown, but the third generation was not brought to maturity by reason of incidents attendant upon my removal to the Desert Laboratory in 1906.

The results obtained with *Oenothera biennis* were much more conclusive, and have been followed in such manner as to leave but little doubt as to the nature and character of the changes induced. Among the seedlings grown from seeds produced by ovaries treated with a zinc solution, early in 1906, was one (erroneously given as

two in other publications) that was distinguishable as soon as the cotyledons had attained full expansion, these organs being broader and of a more vivid green, which was also characteristic of the leaves of the rosette. The plants were kept under close observation until maturity, and guarded seeds were obtained. Every



FIG. 1.—*a, a*, Rosettes of induced derivatives of *Oenothera biennis* three months old; *b*, rosette of *O. biennis* of same age.

stage of their ontogeny was characterized by features which allowed them to be readily distinguishable from the parent. Successive generations were cultivated in the New York Botanical Garden, in the open, under lath shelters, in glass houses, and at the high mountain plantation of the Desert Laboratory, as well as at the Acclimatization Laboratory, Carmel, California, the close of the fifth generation now having been reached, with no diminution of the degree of divergence by which the new form was first recognized. (See figs. 1 and 2.)

The following formal descriptions were prepared from plants grown in New York under conditions as nearly identical as it was possible to secure them:

OENOTHERA BIENNIS, average form.

Mature rosette.—Leaves ample, rather copiously fine pubescent, the larger ones about 27 cm. long, 6–7 cm. wide; blades oblong to elliptic, or slightly broadened upward, unevenly repand-denticulate and most rather jagged toothed near the base, the petioles relatively stout.

Adult plant.—Plant luxuriant, mostly 1 m. tall or less; stem slightly uneven, but scarcely channeled, hirsute with spreading-ascending somewhat rigid hairs, copiously branched throughout, the lower branches decumbent, the upper ones spreading or curved upward; leaves very numerous, 1.5–2 dm. long near the base of the stem; blades elliptic-ob lanceolate to elliptic-lanceolate; shallowly but rather prominently toothed, and often jagged toothed



FIG. 2.—Rosette of induced derivative of *O. biennis* five months old; compare with pl. 3, Publ. no. 24, Carnegie Institution of Washington. 1906.

near the base, acuminate, those of the upper cauline leaves mostly elliptic, acute, sessile, or nearly so; bracts mainly lanceolate, narrowed or rounded at the base; conic portion of the bud 14–18 mm. long, finely pubescent, the free tips of the sepals about 2 mm. long; hypanthium 2–3 cm. long, 5–6 mm. wide at the mouth, nearly terete, sparingly pubescent or glabrate; sepals 15–20 mm.

long, much shorter than the tubular portion of the hypanthium, the free tips 4-5 mm. long; petals rather delicate, 12-16 mm. long, truncate or slightly emarginate at the apex; filaments 8-10 mm. long; anthers 7-8 mm. long; pistil shorter than the stamens; stigmas 4-5 mm. long; capsule 3-3.5 cm. long, 7-7.5 mm. in diameter at the thickest point, finely pubescent, slightly curved, markedly narrowed at the apex.¹

It is to be seen from the above description that *O. biennis* is capable of self-fertilization by reason of the superior length of the stamens, a fact that was demonstrated in the experimental grounds. To secure purely fertilized seeds, it was only necessary to inclose the inflorescence in a parchment bag during the opening of the flowers.

DERIVATIVE.

Mature rosette.—Rosette 20 cm. or more in diameter, flat and quite symmetrical; leaves 9-13 cm. long; blades broadest above the middle, 3-3.5 cm. wide, dark green and shining above, pale beneath, minutely pubescent on veins, some of mid veins reddish above, more or less irregularly and sharply denticulate to quite near the base of the margined petioles, margins wavy, undulate, apex of the leaf somewhat twisted.

Adult plant.—Main stem 60-75 cm. high; stem stout, reddish, somewhat angled, minutely appressed-pubescent, interspersed with somewhat larger spreading cilia; branches starting from base of plant all the way up to top, numerous, 10-15 cm. long; stem leaves 7-10 cm. long, oblong-lanceolate, broadest about the middle, 2-3 cm. wide, bright green, shining above, paler beneath, and pubescent on veins, irregularly and sharply denticulate and somewhat wavy margined; bracts varying from oblong to lanceolate, those of lower branches oblong, acute, 1.5-2 cm. wide, those of upper branches 3-4 cm. long, narrowly lanceolate, acute, shining, and glabrate. (See plates XIV-XVI.)

The transference of the parent and derivative to various localities mentioned has resulted in some exceedingly interesting reactions in which fundamental differences have been displayed. In New York and Tucson, the derivative has wider leaves of a more

¹ Publication no. 24, Carnegie Institution of Washington. 1905.

vivid green than the parent, giving an effect of greater luxuriance. The derivative endures the climate of the mountain plantation better than the parent. In both places the derivative uniformly exhibits a greater amount of red in the leaves than the parent. At Carmel the reddish color is accompanied by a yellowish tinge, the green of the parent remaining practically unchanged. The parent is characterized by an excessive development of the basal



FIG. 3.—*a*, Flowering shoots of *O. biennis*, with broad leaves and short heavy upper branches, grown in equable climate of Carmel, California; *b*, flowering shoot of induced derivative, with narrow leaves and long slender uppermost branches, grown at Carmel.

branches at this place, which are heavy, robust, very leafy, and terminated by dense broad rosettes or by inflorescences. Here, as elsewhere, the capsules are longer than those of the derivative (see pls. XV and XVI) and are more noticeably angled. The derivative grown at Carmel bears numerous branches, which are longer above than in the parent, and are more ascendant, terminating in dense tufts of small reddish bractlike leaves or inflorescences. The capsules of the derivative at Carmel are generally few-seeded. This may be ascribed to the fact that the pistils here are generally longer than the stamens and are exerted from the bud, thus preventing

self-fertilization. The derivative is thus seen to differ from the parent in every stage of ontogeny and reproduction. The differences in question have been maintained through five generations and four sets of climatic and soil conditions.

A few hybridizations of derivatives with the parent have been made, with the result that the cross is found to be intermediate, being more vigorous and showing greater leaf-development than either parent, features which are also displayed in the second generation. The entire set of structural and physiological differences, together with the results of the cross with the parent, points to the conclusion that the derivative is a genotype different from that of the parental form, to which, of course, it stands most closely allied, but with which it does not intergrade.

The successes with these two forms inspired an extended range of experiments with a number of species of widely diversified morphological type, principally characteristic of the arid regions, from 1906 to the present time. Among these were included *Eschscholtzia*, *Argemone*, *Physalis*, *Covillea*, *Carnegiea*, *Mentzelia*, *Opuntia*, *Anemone*, *Amsinckia*, *Pentstemon*, *Echinocereus*, *Echinocactus*, *Sphaeralcea*, *Nicotiana*, *Fouqueria*, *Solanum*, *Kallstroemia*, *Mimulus*, *Phytolacca*, and *Brodiaea*. In addition, diligent watch has been kept for ovaries in which the stings of insects made at an early stage have resulted in serious malformations, with the view of testing probable action upon ovules contained. Only one set of seeds has been secured in this manner so far, and no deviations from the normal were found in the progeny arising from them.

In 1910 some new methods of treatment were tested, by which vapors of various substances, including bromine, were allowed to act upon inclosed inflorescences with eggs and ovules in various stages of development. The fatalities were large, but several progenies from this treatment are now under observation. Practically all plants were grown as they had become established naturally, and no effort was made to secure pollination except in one or two instances in *Pentstemon*. The proportion of losses from various causes was large in all cases. Operations were fairly successful in *Pentstemon*, but the stalks bearing ripening capsules were

harvested so completely by rock squirrels that, out of the hundreds on the slopes near the laboratory, only two or three were allowed to stand in place until the seeds were escaping from the capsules. The three surviving treated stalks of this plant that were saved were preserved by wrapping the stems in cloth. The losses in *Eschscholtzia* were very great, by reason of the quick response of this plant to injuries. *Echinocereus* failed to set a single fruit that had been treated during the first year, although quantities of seeds from treated ovaries have since been secured. Several dozens of ripening capsules of *Argemone* were destroyed by birds; *Mentzelia* matures but few seeds in each capsule; *Opuntia* fails to set fruits in many cases, owing to the injurious effects of the operation and failure to pollinate. *Carnegiea gigantea* drops many flowers that have been operated upon and fails to pollinate many, so that not more than 12 or 15 per cent of the operations were successful with this plant.

These data concerning the fatalities encountered are of interest, since they deal with plants wholly in a state of nature, and represent with fair measure the chance of survival in similar cases that might occur without human intervention.

Some attention has already been given to the conditions found in *Pentstemon Wrightii*, a small beard-tongue native to southern Arizona. This plant displays a wide range of variability in its various habitats. The plants treated on Tumamoc Hill, however, are restricted in the range of somatic characters, their progeny from treated ovaries displaying many supposedly new qualities. A most diligent observation has been made of the wild plants to distinguish naturally recurring characters from those induced. It now seems fairly certain that some new characters are found in the treated progenies. The actual examination of these forms is fraught with great difficulty, since it has not been found possible to secure fertilization in guarded inflorescences, due probably to the fact that the action of visiting insects has not been correctly imitated.

It is evident that the operations described above entail the introduction of reagents into the complex ovular mechanism, and no rational interpretation would be possible without an analysis of

the behavior of the fluid and its possible contact with the main or accessory reproductive elements. First of all, it is important to determine whether the solutions affect the egg cells or the pollen elements, and a number of tests were made with dyes for this purpose. The large ovaries of the giant cactus (*Carnegiea gigantea*) offered some excellent opportunities for testing these points.

The introduction of reagents into the ovaries of this plant was accomplished by thrusting the tip of a needle of a syringe diagonally downward into the cavity through the wall, and then by a steady pressure of the plunger perhaps as much as 0.4 to 0.6 cc. of solution was forced in, setting up a pressure that in some instances increased the external dimensions of the ovary, and the withdrawal of the needle was often followed by the ejection of some of the fluid, but the high turgidity of the walls soon closed the aperture or perforation.

The flowers of *Carnegiea gigantea* ordinarily open in the morning and attract a variety of bees and small gnats, the former probably being instrumental in pollination. Plants taken to the New York Botanical Garden in 1902 did not set seeds unless pollinated by hand. The flowers open in the morning and close with the day when the temperature is above 80° F., but on cooler or cloudy days the flowers may remain open during a part or all of a second day.

The style is as much as 5 or 6 cm. in length, and the pollen tube arising from grains falling on the stigmatic surfaces seems to take nearly a day in effecting fertilization, although exact observations on this point could not be made. It was deemed best, therefore, to inject solutions into the ovaries at any time between 10 A.M. and 4 P.M., thus securing the possibility of affecting the egg apparatus, or the pollen tube as it advanced.

The introduction of methyl blue at this time was followed by its absorption by the inner walls of the locule, and its conduction to the apex of the ovarial cavity at the base of the style in such manner that entering pollen tubes must pass through the impregnated layer, and would be subject to the action of free coloring agent, whether traveling intracellularly or intercellularly. That

it was colored was proved by examination of material a day later, when many stained filaments could be seen. Beside this, the stain was taken up by the concave flanks of the ultimate placental branches which were stained very deeply, and which by their conductive action carried a large quantity of the reagent into the ovule, where it spread between the outer and inner integuments, but it was separated from the nearest portion of the egg apparatus by several layers of cells. Micropylar structures were stained but sparingly when the reagent was introduced into the bases of opening flowers as above.

If, however, the injection was made on the day previous to the opening of the flower or earlier, the placental stalks were not stained so deeply, the amount introduced into the ovule being very small or mostly none at all. On the other hand, the inner integument at the micropylar orifice was deeply stained, so that any pollen tube entering through this structure would certainly encounter the reagent. The conducting tissue on the inner surface of the locule was deeply stained at this stage, and by its action much of the color was conducted to the apical region through which the pollen tube must pass.

It is to be seen, therefore, that the placental stalk presents a concave flank most highly absorbent and conductive at the time that the egg apparatus is complete and awaiting fertilization. Before this time, the introduction of a reagent results in greater affection of the endostome and greater accumulation of the coloring matter in the basal portion of the pistil through which the pollen tubes must pass. The probabilities would be greatly in favor of a reagent acting upon the pollen nucleus when introduced at this stage, to the total exclusion of any direct effect upon the embryo sac. Injections on the day of fertilization, at a time when most of the successful operations were performed, resulted in some of the solution going into the ovular structures, but not into such close contiguity that the embryo sac might be supposed to be affected. In a few instances the endostome was also stained, while the tissue through which the pollen tubes pass into the locule accumulated the reagent.

Oenotheras were injected with methyl blue at the Desert

Laboratory in June 1907 to ascertain the probable mechanical effects by which divergent derivatives had been induced in two genera. Colored solutions introduced into the ovaries the day before fertilization showed but meager effect in comparison with the actual results of injection in the cactuses. The stain was found adhering to the outer layers of the ovule, in which the embryo sac lay deeply buried. In no instance was anything like a marked penetration observed. The placental stalks were stained in a few instances, and rather deeply, and this offers the only shadow of a clue as to possible effects of the introduced reagents. The number of ovules affected in any way well accords with the comparatively meager effects secured. It was noted also that the rupturing of the ovarial walls freed numbers of crystals of calcium carbonate, which were partly dissolved by many of the reagents and would thus complicate hypothetical reactions.

The introduction of methyl blue solutions into ovaries of *Mammillaria* on the days the flowers were opened, resulted in staining the papillar cells which project from the sharp angles of the funicular or placental stalk, which is curved in such manner that a pollen tube would pass among them, probably coming into the closest contact with their mucilaginous walls. Here, as in *Carnegiea*, the introduction of a foreign substance would place the greatest chance of affection of the germinal elements within the pollen tube. Further tests were made with a solution obtained by allowing powdered carmine to stand in distilled water. The introduction of the reagent into the ovaries of the flowers that had opened was followed by a general absorption of it by the absorptive cells of the concave flanks of the funicular stalks, and by the underlying cells, with only a slight affection of the ovule and only an occasional reaction from endostomes. Injections of flowers the day before opening, however, gave more marked results. In this case, not only was the dye taken up by the conductive systems lining the locules as in the case above, but the stain had traveled up the base of the pistil for as much as a centimeter. Furthermore, the reagent was not only taken up in quantity by the funicular stalk, but it had been conducted into the ovule, where much of it had accumulated between the outer and inner integu-

ments. Beyond this it could not be traced, although it seems reasonable to suppose that some action extended beyond. At the same time, numerous endostomes could be detected which had taken on a marked stain. Not only were the external cells colored, but the action extended inward some distance.

The study of the movements of dyes yields some profitable suggestions as to the probable mechanical movements of reagents introduced into ovaries for the purpose of affecting the egg apparatus or the pollen tube. The coloring matter was not seen to penetrate farther than a point separated by five or six protoplasts from the egg nucleus. The pollen tube carrying the fertilizing nucleus, however, may be compelled to pass through or among cells taking up any foreign substance, so that only the two walls and the cytoplasm intervened. It seems, therefore, that the greater weight of probability lies on the side that the proembryonic affectation of the germinal elements of a seed plant is one in which the possible changes are to be supposed to be due to the action of the reagent on the pollen nucleus rather than on the embryo sac.

The care of treated plants until the seeds in treated ovaries have matured and may be harvested has absorbed much effort, since in many species the plants may ripen a few seeds daily, and collections must be made frequently. Next after the harvesting of the seeds, sowings must be made at the proper time of the year. In the case of species of the desert it has not been found profitable to attempt germinations except at the customary time, else enormous fatalities may occur. Many of the forms which offer particularly favorable conditions for ovarial treatments are slowly developing perennials, which need several years to reach the stage in which they may produce seeds and thus furnish a second generation.

At the present time, seedlings from treated ovaries are under observation as follows: *Echinocereus Fendleri*, *Echinocactus Wislizeni*, *Brodiaea capitata*, *Fouqueria splendens*, *Sphaeralcea pedata*, *Pentstemon Wrightii*, *Phytolacca decandra*, *Opuntia discata*, *Carnegiea gigantea*, *Amsinckia spectabilis*, and *Solanum eleagnifolium*. Of these, lots from successive seasons are under observa-

tion from two species, in which some species are represented by two or more different treatments.

The announcement was made in 1908 that some divergent characters were seen in a treated progeny of *Cereus*. The plant in question, by the incessant changes of nomenclature, is known at the time of this writing as *Echinocereus Fendleri*. The progeny is coming into bloom, and while one of the individuals diverges widely beyond the observed range of fluctuating variability, it cannot yet be definitely stated whether or not the characters displayed are permanently heritable or not. The individual in which they are represented is of normal vigor, and is not in any ordinary sense monstrous or teratological.

It may be readily apprehended that any theoretical interpretation of the action of the reagents employed in this series of experiments is extremely difficult. The question as to whether the embryo sac or the generative nucleus of the pollen tube is acted upon is, withal, a purely mechanical consideration. The real problem is the nature of the alterations induced by the action of the compounds to which the test plants are subjected.

Some of the earlier results with *Raimannia* were obtained with solutions of cane sugar, not of tested purity, however, and applied with built-up metal syringes, and corrosion may have occurred to such an extent as to make the action similar to that in which solutions of metals and halogens were used in proportions of 1 to 10,000 or 1 to 50,000 of distilled water. The application of zinc and iodine solutions in the more carefully guarded operations may have affected the reproductive protoplasts in various ways. The chief difficulties in the way of theoretical interpretations consist in the fact that the direct action of the reagents cannot be followed in the deeply buried reproductive elements. It can only be said that the reagents might alter the dissociations in the cell, while not entering it, or perhaps only in the minutest quantities, and the properties of an egg might well diverge with changes in the relative number of free ions of various kinds in its compounds. This assumes, of course, a direct connection between the chemical constitution of the cell and the properties it displays. The entire effect might be due simply to altered

permeability of the limiting membranes of the protoplasts or of the vacuolar sacs.

Experimental studies such as are here described lead the investigator into the consideration of two phases of the subject. One is concerned with the demonstration of induced hereditary alterations and the study of their behavior in pedigreed strains, in hybridizations, and under various environic conditions. The other includes a consideration of the mechanism by which an environic agency affects the physical bearers of heredity. Both comprise some important and interesting possibilities in evolutionary science.

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EARLIER PAPERS BY THE AUTHOR ON RESULTS OF OVARIAL TREATMENTS

1. Heredity and the origin of species. *Monist*, Jan. 1906; reprinted in advance Dec. 1905, and as Contribution No. 80 of the New York Botanical Garden, 1906.
2. Heredity and environic forces. Vice-presidential address before Section G, A.A.A.S., at Chicago meeting, Dec. 30, 1908; reprinted in advance of annual volume.
3. Heredity and the origin of species. *Smithsonian report* for 1908, pp. 505-523; issued in 1909.
4. Physiology of genetics. Sixth year book, Carnegie Institution of Washington, p. 62, 1907; seventh year book, p. 63, 1908.
5. Alterations in heredity induced by ovarial treatment. Eighth year book, Carnegie Institution of Washington, p. 59, 1910.
6. The direct influence of environment. *Fifty years of Darwinism*, p. 114, 1908.
7. Origination of self-generating matter and the influence of aridity upon its evolutionary development. *Outlines of geologic history*, by WILLIS and SALISBURY, p. 278, 1910.
8. Environic response. *Amer. Nat.*, Jan. 1911; also *Science*, Jan. 20, 1911.

EXPLANATION OF PLATES XIV-XVI

PLATE XIV.—A, rosette of *Oenothera biennis* at Desert Laboratory, 1910; B, rosette of induced derivative.

PLATE XV.—*Oenothera biennis*: 1, leaf from young rosette; 2, leaf from rosette four months old; 3, leaf from lower part of mature rosette; 4, leaf



MACDOUGAL on OVARIAL TREATMENTS



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from upper part of mature rosette; 5, stem leaf; 6, bract; 7, unopened bud; 8, flower with petals removed; 9, petals of maximum size; 10, mature capsule; 1-5, one-half natural size; 6-10, natural size.—From Publ. no. 24, Carnegie Institution of Washington. 1905.

PLATE XVI.—Derivative of *Oenothera biennis*: 11, leaf of young rosette; 12, leaf from mature rosette; 13, leaf from mid-stem; 14, leaf from upper part of stem; 15, bract; 16, flowering branch; 17, flower stripped of corolla; 18, petals; 19, capsule and bract.

SOME FEATURES OF THE ANATOMY OF THE FOLIAR BUNDLE¹

EDMUND W. SINNOTT

(WITH PLATE XVII)

Although the vascular system of the leaf in the Cycadaceae has for some time been recognized as a region where primitive structures, notably centripetal wood, have persisted longer than anywhere else in the plant, the general principle of the conservatism of the foliar organ has only recently been more widely extended and found to hold good for all the main groups of vascular plants: Lycopsidea, Filicales, Gymnosperms, and Angiosperms. The position of the protoxylem in relation to the later formed elements of the wood is very constant in the large orders, but its importance in determining phylogenetic relationships seems often to have been overlooked. A brief summary of the structure of the leaf trace and foliar conducting system of all families of vascular plants, with special reference to the position of the protoxylem, and a more particular account of conditions in the living Cycadaceae, the only existing gymnosperms with centripetal wood, together with a discussion of the bearing of the results on our views as to the evolutionary history of the higher plants, is the purpose of the present paper.

That the base of the leaf trace, since it is least subject to changes in external conditions, should retain ancestral structures longer than does any other portion of the foliar system seems logical, and this has been proven to be true in several groups of vascular plants. It is therefore in this region that we should look for the primitive structure of the foliar bundle.

In all the Lycopsidea where the anatomy of the leaf is known (*Equisetum*, *Lycopodium*, *Selaginella*, *Phylloglossum*, *Tmesipteris*, *Psilotum*, *Isoetes*, *Lepidodendron*, and *Sigillaria*), the vascular strand at the base, and in the majority of instances throughout the lamina, of the leaf, is a single concentric strand, roughly circu-

¹ Contribution from the Phanerogamic Laboratories of Harvard University, no. 33. *Botanical Gazette*, vol. 51]

lar in cross-section, and with one median mesarch² protoxylem group. This condition also occurs at the base of the leaf trace in the Osmundaceae and Ophioglossaceae, and it apparently is present at the node of the Botryopterideae (1), and therefore seems to have been the primitive one for these families. It is very evidently the earliest type of foliar strand in vascular plants, and has persisted almost unchanged in the microphyllous Lycopsidea, but in the megaphyllous Pteropsida has undergone extreme modification.

A very ancient type of leaf bundle has recently been investigated by BERTRAND in his account of the anatomy of the leaf in the Zygoterideae (1), one of the three families of the Botryopterideae, those simple protostelic ferns which clearly stand close to the ancestors of the modern Filicales. The early condition of the leaf trace in this group is of importance as representing the primitive one for all ferns. This has been found by BERTRAND in the simpler forms of the Zygoterideae, such as *Clepsydropsis* and *Asterochlaena*. These genera possess a leaf bundle which is concentric and rather elliptical in shape, and which contains at either end an island of parenchyma imbedded in the xylem. Around the island are placed the protoxylem elements, which are irregularly scattered in the former genus and in two distinct groups in the latter. BERTRAND has established a very complete series of forms between this type of leaf strand and the more complicated bundles of the remaining Botryopterideae, all of which seem clearly to have been derived from the simple diarch and mesarch condition. The original monarch structure persists at the base of the trace.

In a recent paper (9) the writer has endeavored to show how the leaf bundle of the modern Filicales has been developed from that of these primitive Zygoterideae. Aside from the change in shape and the breaking up of the strand into separate bundles, the most notable difference between the modern forms and their ancestors

² The term "mesarch," as used in the present paper, is descriptive of any protoxylem group, whether situated at the axis of the stem or not, which is surrounded by metaxylem. "Endarch" describes any condition where the protoxylem is not at the axis and where there is no metaxylem (centripetal wood) formed on its inner face. "Exarch" describes any condition where all the primary metaxylem is formed on the inner or adaxial side of the protoxylem.

is in the position of the protoxylem. In the petiole of every living genus of ferns except *Lygodium*, the first-formed tracheids are endarch, and the upward development of the filicinean leaf seems to be uniformly marked by the disappearance of its centripetal wood. At the base of the leaf trace in many ferns a mesarch condition still persists. Here the protoxylem is usually simply mixed indiscriminately in the metaxylem, but in those rather rare cases where it shows a definite attachment either way, it almost always becomes continuous with the centrifugal wood. The base of the leaf trace of *Thamnopteris*, a primitive osmundaceous fern, as described by KIDSTON and GWYNNE-VAUGHAN (3), is a good example of this. Endarchy and the attachment of the protoxylem to the centrifugal wood are therefore distinctive characters of the advanced filicinean foliar bundle.

The close affinity of the Cycadofilices to the ferns is manifest in the structure of the leaf trace as well as in many other characters, and there seems good reason to believe that the foliar strand in this group of early seed plants has been derived from a bundle very similar to that of *Clepsydropsis* or *Asterochlaena*.

The most primitive genera of the Cycadofilices and those which approach the ferns most closely in all their characters are *Calamopitys*, *Lyginodendron*, and *Heterangium*. In *Calamopitys*, which is a very ancient form, going back to the Devonian, the base of the leaf trace, while still one of the bundles which surrounds the pith, is a single strand, with a cluster of protoxylem mixed with parenchyma at its center. In most species the centripetal wood becomes reduced at the very base of the bundle, and in *C. Beinertiana*, as described by SCOTT (5), it is actually broken through, the protoxylem becomes continuous with the centrifugal wood, and an endarch condition results. As the single mesarch trace leaves the stele, its protoxylem group divides into two parts, which lie near the outer face of the bundle, and each of these soon divides again into two. The trace on becoming free splits equally into two diarch, mesarch, and concentric strands, which pass out through the cortex. In the base of the petiole these split up into an arc of six bundles. The primitive monarch condition is therefore present at the very base of the trace; this soon takes on the diarch structure

of *Clepsydropsis*; and this in turn assumes a tetrarch condition, the striking similarity of which to the bundle of *Asterochlaena* has been noted by BERTRAND. It is noteworthy that the typical modern fern character of endarchy is present only in the stem. In the leaf trace in the cortex, the first formed elements of the wood seem to be clearly connected with neither face of the bundle.

Conditions in *Lyginodendron* are very similar. The trace at its base is monarch, and though true endarchy apparently never occurs in this genus, the protoxylem group, which lies near the outer edge of the bundle on the abaxial side of an immersed island of parenchyma, is always continuous and in seriation with the narrow arc of centrifugal wood. This relation of the protoxylem to the metaxylem persists throughout the course of the leaf trace in the cortex, but is apparently lost in the petiolar bundle, where the earliest tracheids show no definite attachment to either the inner or the outer wood.

The single protoxylem group soon divides into two (fig. 6), as in *Calamopitys*, and the trace in a short time also separates into two equal parts, which shortly become diarch. These four clusters of protoxylem are all near the outside of the metaxylem, but are seriated with the centrifugal wood if at all. In the petiole the two strands become united by their abaxial ends into a tetrarch arch, which becomes gradually wider and more flattened and soon contains eight to ten protoxylem groups, all of which are clearly mesarch. This wide bundle often becomes divided into several distinct strands, which in the upper part of the rachis come together into a tetrarch and finally triarch and mesarch bundle, such as is figured by SCOTT in his description (6). It is noteworthy that in the petiole and rachis the abaxial elements are always smaller than the adaxial ones, a condition which is often found in the leaves of living ferns.

The structure of the trace in *Heterangium* is very similar to that in *Lyginodendron* except that it often remains undivided. The mesarch protoxylem here as well as in the stele is always in seriation with the centrifugal wood.

It is clear that in these three genera we have to deal with plants showing a strikingly close resemblance in the lower and more

primitive portions of their leaf bundles to conditions which prevailed in the foliar strands of the early Botryopterideae, and it seems reasonable to suppose that this resemblance indicates a phylogenetic relationship between the two groups. These cycad-ferns, however, show their advanced condition by the possession of a much more complicated petiolar system, and by displaying the tendency shown by modern ferns for the protoxylem to become continuous with the centrifugal wood and to be at last completely endarch.

The remaining Cycadofilices show a very different structure in their leaf bundles. Here the progression, instead of being toward endarchy, is all toward exarchy, and the primitive mesarch trace with protoxylem near the outside loses its narrow zone of centrifugal wood, and its protoxylem becomes continuous with the centripetal wood, thus forming a direct contrast to the trace of *Lyginodendron*. The *Myeloxylon* type of bundle characteristic of the petioles of *Medullosa* and *Sutcliffia* shows clearly this exarch condition, though *Colpoxylon*, which often possesses only a single vascular cylinder in its stem and which is therefore probably more primitive than the other two genera, shows traces of centrifugal wood and the ancient mesarch structure. In all these genera the petiolar vascular system consists of a large number of bundles more or less irregularly arranged, but, in *Medullosa* at least, the base of the leaf trace is a single strand possessing one or more groups of protoxylem which seem to be slightly imbedded in the metaxylem.

In *Megaloxylon* the base of the leaf trace is the only part of the foliar strand of which the structure is known, and it is here a single exarch bundle.

Ptychoxylon Levyi, one of the Cycadoxyleae, shows a closer approach to the primitive Cycadofilices, for here the trace is a double one, each part of which, however, instead of being mesarch is clearly exarch.

In those primitive gymnosperms of the Palaeozoic included in the cordaitan alliance, we find the same exarch structure in the leaf bundle, which almost always consists at its base of two strands. In *Poroxylon* this pair of monarch bundles, which ultimately unite at their very base, are carried well down into the stele,

the primary wood of which is thus entirely centripetal. In the petiole and blade of the leaf, the double trace divides into a series of parallel strands, each of which possesses a mass of exarch primary wood, on the outer side of which, except at the edges of the leaf, is a zone of secondary xylem, just as in the leaves of living cycads.

In *Mesoxylon*, a new genus recently established by SCOTT and MASLEN (7) to include forms intermediate between *Poroxylon* and the Cordaiteae, we see in the stem the beginnings of the endarch condition of the higher gymnosperms. The double leaf trace is still exarch, the protoxylem being in seriation with the centripetal wood which, in the very lowest part of its course, in several species, becomes much reduced and may finally disappear, leaving as the only relic of the primary wood the cluster of protoxylem, which is separated by parenchyma from the centrifugal secondary xylem. The structure of the leaf trace and foliar bundles in this genus is the same as in *Poroxylon*.

In the case of Cordaites, however, the typical stem structure of the modern gymnosperms makes its appearance, for here the protoxylem attaches itself to the centrifugal wood, which is almost, if not quite, entirely secondary. In the double leaf trace, however, well developed centripetal primary wood appears, with exarch protoxylem on its outer face. In the leaf blade the veins are clearly exarch. In certain species centrifugal xylem is present here, separated by parenchyma from the protoxylem and probably secondary in origin, but this is absent in the simpler forms such as *C. principalis*, where the structure is strikingly like that of a *Medullosa* bundle.

There are certain other fossil plants, probably rather closely related to *Poroxylon* and the Cordaiteae, which possess a somewhat similar type of leaf trace and primary wood, and which have been grouped by SCOTT under the family name of Pityeae.

In the genus *Pitys* the trace shows signs of bifurcation as it passes out, and it is clearly mesarch, as are the medullary strands of primary xylem. The bundles are all small, however, and the protoxylem shows no tendency to align itself with either the centrifugal or centripetal wood, showing in this respect a primitive condition.

Dadoxylon Spenceri shows considerable resemblance to *Poroxylon*, for its leaf trace, at first single, becomes double before leaving the stele, and possesses well developed primary centripetal wood, on the outer face of which occurs the exarch protoxylem. At the very base of the trace, however, this primary wood disappears and an endarch condition results.

It seems highly probable that the living Coniferales have been derived from plants closely related to the Cordaitales, but that, in the course of their development, the modern members of the group have almost entirely lost the centripetal primary wood so characteristic of their ancestors. In the cretaceous genus *Prepinus*, however, JEFFREY (2) has recently described an intermediate condition between ancient and living forms, for in the leaf of this primitive pine there is abundant centripetal wood. Though the protoxylem is adjacent to this, it is apparently in seriation with the centrifugal part of the bundle, which is very probably modified secondary xylem, as indicated by the presence of abortive medullary rays. In this case, apparently, the first-formed tracheids had assumed the typical coniferous position before the disappearance of the centripetal xylem. We shall find a very similar condition at the base of the petiole in living cycads.

Among the higher modern gymnosperms, the only occurrence of centripetal wood is in *Ginkgo*, where it is present as scattered tracheids, not in connection with the protoxylem, in the cotyledons, vegetative leaves, and anthers. This genus, which on other evidence is accounted one of the most primitive of the existing gymnosperms, also possesses a double leaf bundle and a wide, parallel-veined, rather cordaitean lamina.

The occurrence of a double foliar strand, in the more ancient of the living conifers, seems without much question to be the persistence of such a double trace as is found at the base of the leaf in the Cordaitales. The double foliar bundle found by Miss THOMAS (12) in the seedlings of many angiosperms is probably also an indication of a primitive condition. The leaf trace in the adult members of this group takes on a great variety of forms, and never displays the true centripetal xylem or "cryptogamic wood" of the early gymnosperms.

The mesozoic Cycadophyta, exemplified by the two genera *Cycadeoidea* and *Bennettites*, though showing in their cauline central cylinders the endarch condition characteristic of modern cycads and other gymnosperms, still possess primitive features in their leaves. The foliar trace as it departs from the stele is a single arched bundle. In the base of the petiole of *Cycadeoidea*, as observed by WIELAND (13), and of *Bennettites Gibsonianus*, as observed by SEWARD (8), there is a considerable amount of primary centripetal wood and of radially arranged secondary centrifugal wood, with protoxylem between the two. The seriation of the protoxylem is impossible to make out, but it was doubtless exarch, as in modern cycads. The centrifugal wood apparently diminished in amount in the upper part of the petiole. The structure of the vascular bundle in the lamina of the leaf is described by WIELAND in *Cycadeoidea* as "mesarch" and very similar to that in living cycads.

Certain recent discoveries by Miss STOPES and FUJII are of importance in this connection. The leaf blade of *Niponophyllum*, as described by these authors from the Cretaceous of Japan (11), is parallel veined and possesses collateral exarch vascular bundles with no centrifugal wood, thus presenting a very close resemblance to certain of the more simple types of leaf among the palaeozoic Cordaitales.

In *Nilssonia orientalis*, another Japanese cretaceous form described by Miss STOPES (10), the leaf blade is pinnate, having a strong midrib from which come off parallel lateral veins. The vascular strands here also seem to be clearly exarch, with no trace of centrifugal wood. The structure of the stele and of the leaf trace in neither of these forms is known.

The living Cycadales show a close resemblance anatomically to the palaeozoic Cycadoxyleae, notably *Ptychoxylon*. The central cylinder of the stem is always endarch with no centripetal xylem, save for a few scattered tracheids, not connected with protoxylem, in the reproductive axes of certain species. The leaf trace departs as a double bundle, the halves of which soon separate and pass around the stem in opposite directions before entering the base of the leaf, where they divide into a many-bundled arch. Very

primitive structures are retained, as in so many former cases, only in the petiole and blade. The vascular anatomy of this portion of the plant, with special reference to the position of the protoxylem, was investigated by the writer in a considerable number of species.³ The results obtained agree in general with those of METTENIUS (4) and other later investigators.

At the very base of the leaf trace in all the species the primary wood becomes increased in amount at the flanks of the bundle, and two adaxial projections are here formed which finally unite behind the original position of the protoxylem and inclose a small island of parenchyma. The protoxylem either follows one or both of these masses of metaxylem backward, always remaining attached to them, or else swings over to the centripetal wood as soon as the two arms of the latter unite. Just before this change takes place, the bundle presents a close similarity to that of the leaf of *Prepinus*, for both centripetal and centrifugal wood are well developed, and the protoxylem is in seriation with the latter (fig. 5).

The centrifugal wood becomes very rapidly diminished in amount as the bundle ascends, so that in the middle and upper portion of the petiole in many species, such as *Zamia integrifolia* and *Encephalartos Altensteinii*, it is either absent in most of the strands or represented by only two or three elements (fig. 2). It is also noteworthy that, except perhaps at the very base of the petiole, this outer xylem seems to be entirely secondary, as is shown by its relation to the phloem. All but the extreme outer part of this latter tissue is clearly secondary and radially arranged, and the centrifugal tracheids are almost always just at the inner ends of the rows of phloem elements, and seem unquestionably to have been produced by the same cambial activity (figs. 1 and 3). They are usually pitted and not scalariform, as are most of the elements of the centripetal xylem.

³ These include *Cycas verticillata*, *C. media*, *C. celebica*, *C. ruminiana*, *C. circinalis*, *Zamia furfuracea*, *Z. macrophylla*, *Z. Loddegesii*, *Z. integrifolia*, *Z. Skinneri*, *Z. Linderi*, *Z. muricata*, *Z. Seiboldii*, *Ceratozamia latifolia*, *C. mexicana*, *C. kuesteriana*, *Encephalartos horridus*, *E. Altensteinii*, *E. Lehmanii*, *Microzamia spiralis*, *Dioon edule*, and *Bowenia spectabilis*.

The protoxylem is always attached to the primary centripetal wood, which forms the great bulk of every bundle, and it is clearly in seriation with it, the smallest and ringed elements being on the very outside and becoming successively closely ringed, spiral, and pitted as we approach the inner or adaxial edge of the strand (fig. 4). Between the protoxylem and the centrifugal wood there is in nearly every case a row of parenchyma, one or two cells wide, just as in the cordaitean leaves which possess centrifugal wood. The petiolar bundles may vary in shape from narrowly triangular, with the protoxylem carried up on the apex, to almost semi-circular, with the first formed tracheids in the middle of the flat upper side.

The resemblance of a cycad leaf bundle to the foliar trace of *Lyginodendron* has been much emphasized by SCOTT and others. There are apparently two very vital differences between the two, however, for the former has no centrifugal primary wood, as has the latter, and in the cycad leaf the protoxylem is distinctly seriated with the centripetal xylem, and not with the centrifugal, as it is in *Lyginodendron*. The one is exarch and the other mesarch with a tendency toward endarchy. Scattered bundles were observed in several species, where the protoxylem connected the inner with the outer wood, being attached to both. Such cases are doubtless reduced and due to the partial abortion of the separating zone of parenchyma. In all of them the protoxylem remained in seriation with the centripetal wood.

In the leaf blade the centrifugal secondary wood is still further reduced, especially when the bundles become small at the end of a pinna. In several species, such as *Dioon edule*, it is altogether absent, and in no case is it represented by more than three or four cells. These often lose their radial arrangement and tend to cluster round the outer face of the protoxylem cluster. This gives the mesarch appearance, which is probably similar to what WIELAND saw in the blade of *Cycadeoidea*. In the small cotyledonary traces of *Bowenia*, WORSDELL observed a true mesarch structure, which may perhaps be a reversion to the very primitive botryopteridean condition.

Conclusions

The following general phylogenetic conclusions may be drawn from a study of the leaf trace and foliar bundle of vascular plants.

The primitive foliar bundle was a single monarch and mesarch vascular strand. This has persisted in the leaf trace of all the Lycopsidea and in the blade of many of them, thus furnishing further evidence of the unity of the group and of its relatively primitive position.

This type of bundle is present at the base of the leaf trace in the Osmundaceae and in certain of the Ophioglossaceae, which thus seem to have been early separated from the other ferns.

The leaf bundle of the primitive palaeozoic Filicales was a diarch and mesarch one. By the disappearance of its centripetal wood, this has given rise to the endarch foliar strands of living ferns, which have apparently been derived from the more ancient of the Botryopterideae.

The diarch and mesarch leaf bundle is also the primitive one for the seed plants, which were developed along two main lines from forms related to the early Botryopterideae, but which had acquired the seed habit. The members of the first series, including *Calamopitys*, *Lyginodendron*, and *Heterangium*, show the fern tendency for the protoxylem of the stele and leaf trace to become continuous and in seriation with the *centrifugal* wood, and for an ultimately endarch condition to result. The other series, which includes all remaining gymnosperms, and probably the angiosperms, shows in its earliest and most primitive forms the tendency in the vascular system of the stem and leaf for the protoxylem to become continuous and in seriation with the *centripetal* wood, and for an ultimately exarch condition to result.

These two groups are also clearly separated on other evidence. The endarch series are very fernlike in habit, possess seeds of a peculiar type, and show in their petiolar bundles (at least in *Lyginodendron*) that ancestral mesarch condition of the Botryopterideae where the protoxylem shows no preference for either the inner or the outer wood. The early members of the exarch group, however, such as *Medullosa*, do not show such striking resemblances to the ferns, possess seeds of a higher and more

cycadean type, and display an exarch condition not only in the leaf trace but throughout the petiolar system.

The double trace is clearly present in the endarch series, and is also found in most of the exarch forms, including the higher Cycadofilices; *Poroxylon*, *Cordaites*, and their allies; many modern conifers, and the living Cycadales. It seems clearly to have been a primitive character, and to have arisen from a constriction of the single diarch strand which was present in the ancestors of all seed plants.

The endarch line of development apparently ended blindly and did not give rise to the typically endarch higher plants, which were developed along several distinct lines from a plexus of forms in the exarch group possessing a double leaf trace and seeds resembling those of *Medullosa*.

The Poroxyleae, Pityeae, and Cordaiteae came from this plexus at a very remote period. The tendency among this series has been toward the development of a parallel veined leaf, a clearly gymnospermous type of reproduction, and an endarch condition of the central cylinder, together with a wide zone of secondary wood.

The parallel venation of the leaf has doubtless been derived from a pinnate condition, with a two-bundled exarch rachis, a structure which has persisted only at the base of the trace. The cordaitean type of leaf seems to have existed in the Cretaceous, as is shown by the occurrence at that period of such forms as *Niponophyllum*. The genus *Nilssonia*, possessing a simple leaf with a distinct midrib but with clearly parallel lateral veins, shows an intermediate condition between a pinnate cycadean leaf and a parallel veined condition, and gives a suggestion as to how the latter may have been produced.

The cordaitean type of reproduction is unknown in the Cycadofilices, but *Trigonocarpon*, the seed of *Medullosa*, approaches closely the seeds of the Cordaiteae.

The endarch condition of the central cylinder has been caused by the disappearance of the centripetal primary wood of an exarch stem consequent upon the great increase in bulk of the centrifugal secondary wood, to which the protoxylem has finally attached itself.

A second line from the double-bundled *Medullosa*-like plexus of

the exarch group, but one which lies close to the cordaitean alliance, has given rise to the Ginkgoales, the Coniferales, and probably the angiosperms. Centripetal wood persists here only in *Ginkgo*, and in the leaves of such ancient conifers as *Prepinus*. Endarchy is apparently elsewhere universal, although our knowledge of conditions in the earlier forms is very slight. *Ginkgo* and the more primitive conifers possess a double foliar bundle, and all members of both groups have parallel veined leaves. The double bundle also appears in seedlings of certain angiosperms, but this series has otherwise departed very widely from its palaeozoic ancestry.

A third line from our ancient stock gave rise to the cycad-like Bennettitales which flourished in the Cretaceous. The foliar trace here was a single bundle—either the primitive single strand, perhaps comparable to that of *Medullosa*, or a fusion of two—which developed in the petiole and blade into a series of typically exarch bundles with centrifugal secondary wood. The reproductive organs were very specialized, and the group has probably given rise to no living family of plants.

The modern Cycadales perhaps constitute a fourth line from the palaeozoic plexus which, however, lies very close to that of the Bennettitales. They have often been considered as derived from forms related to the Lyginodendreae, but the exarch structure of the leaf bundles and the construction of the seed, which is much more comparable to that of *Medullosa* than to that of *Lyginodendron*, make it very improbable that the latter genus has given rise to the modern family. The cycads are also separated from the Bennettitales by the possession of a double leaf trace and a simple reproductive system. The parallel venation of the leaf suggests the Cordaitales, and, as we have remarked above, *Nilssonia* shows an intermediate condition between the two types of leaf.

It seems probable that the group arose in the late Carboniferous from cycad-ferns possessing a double exarch leaf trace and petiolar bundle, a type of leaf intermediate between the ordinary fern frond and the parallel veined cordaitean condition, and a seed resembling that of *Medullosa*.

There are thus apparently two main groups in the exarch series,

one of which has progressed toward the coniferous type, and is represented by the Cordaitales and the modern Coniferales, and the other of which has produced the cycadean type, as represented by the Bennettitales and the modern Cycadales.

The writer is under much obligation to the authorities of the Royal Botanic Gardens at Kew and of the Botanic Garden of Harvard University for material. He also wishes to express his thanks to Professor E. C. JEFFREY for advice during the course of the work.

This investigation was carried on in the Phanerogamic Laboratories of Harvard University.

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EXPLANATION OF PLATE XVII

FIG. 1.—Petiolar bundle of *Cycas revoluta*, showing the typical cycadean condition, with primary and secondary phloem, primary centripetal xylem, and secondary centrifugal xylem; $\times 150$.

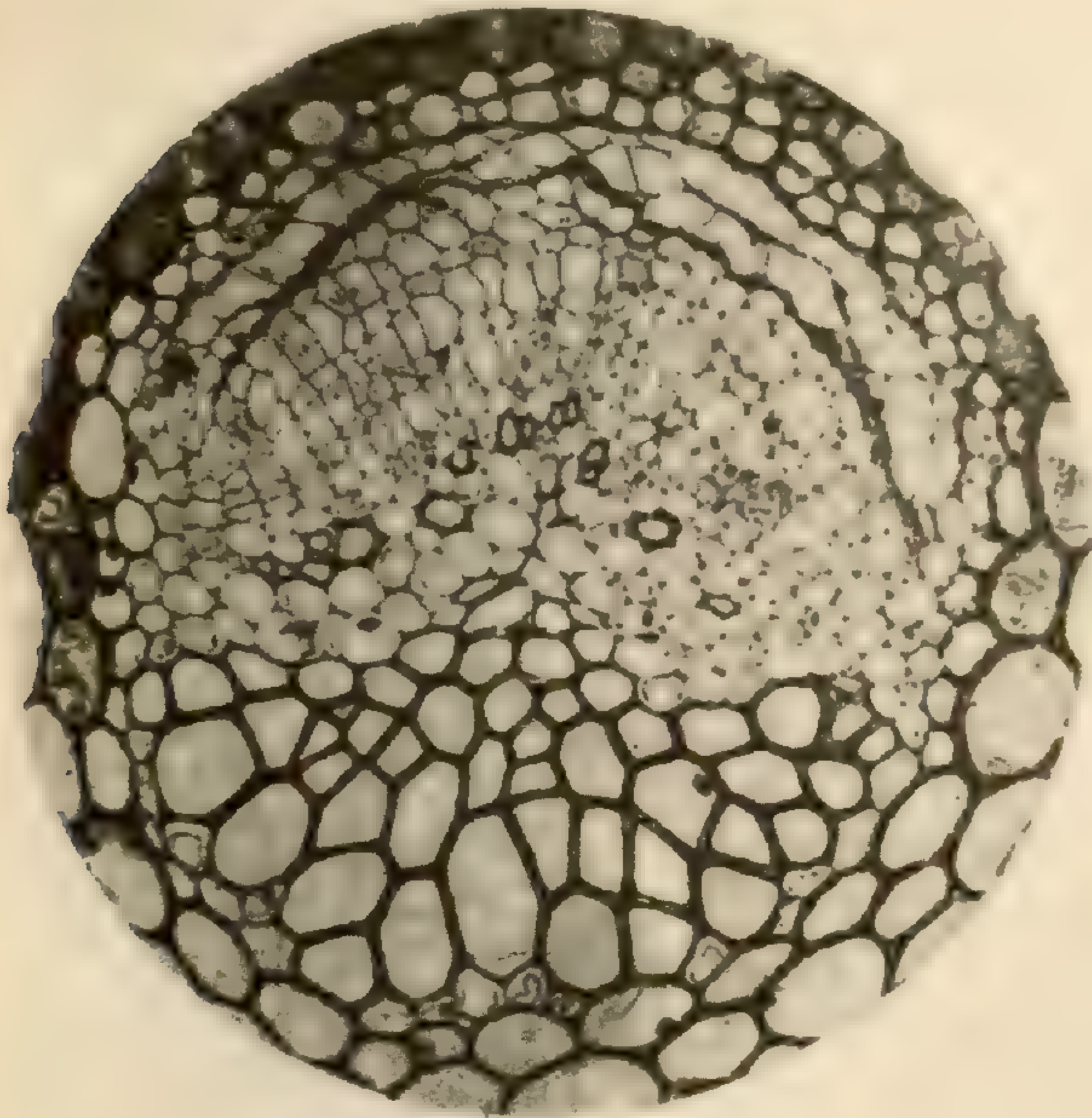
FIG. 2.—Typical petiolar bundle of *Encephalartos Lehmanii*, showing complete absence of centrifugal wood; $\times 250$.

FIG. 3.—Petiolar system of *Zamia Loddegesii*, showing the small amount of centrifugal wood and its radial arrangement.

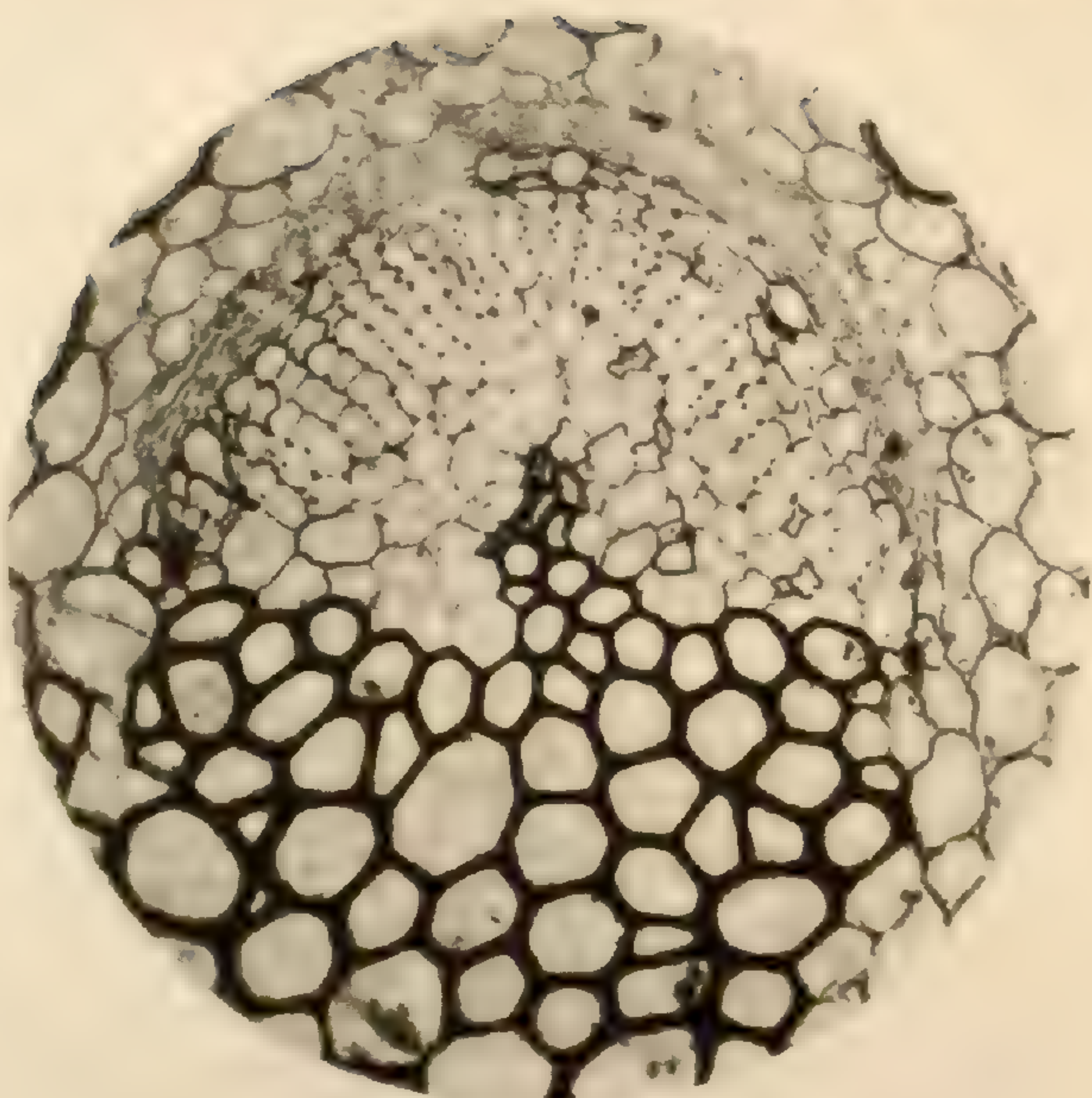
FIG. 4.—Longitudinal section of a bundle of *Cycas revoluta*, with centrifugal wood on the left and centripetal wood on the right; the protoxylem is clearly in seriation with the latter; $\times 100$.

FIG. 5.—Bundle from the base of the petiole of *Zamia macrophylla*, showing the protoxylem attached to both centrifugal and centripetal wood; $\times 120$.

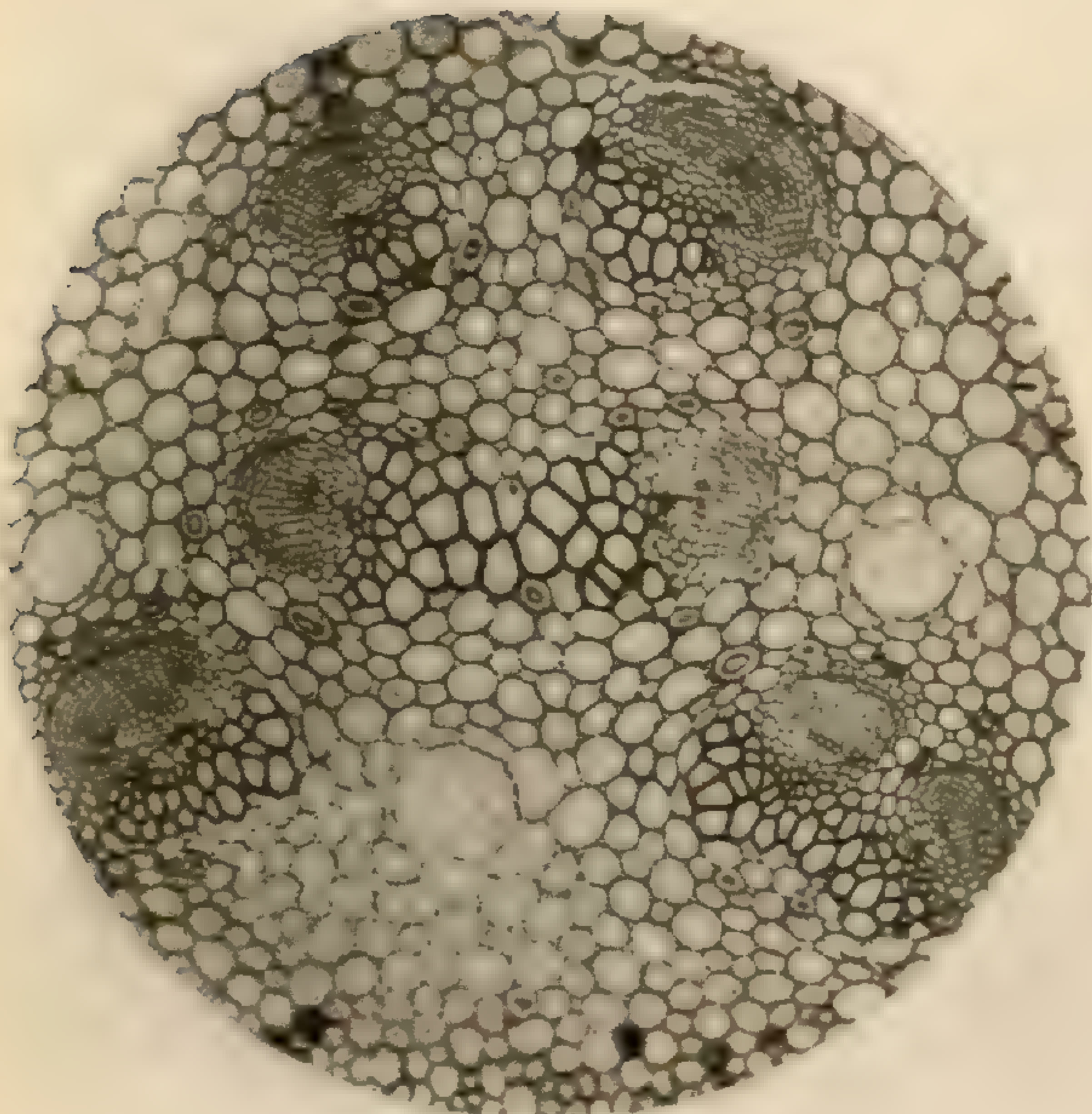
FIG. 6.—Leaf trace of *Lyginodendron* at its separation from the stele, showing the diarch condition; $\times 40$.



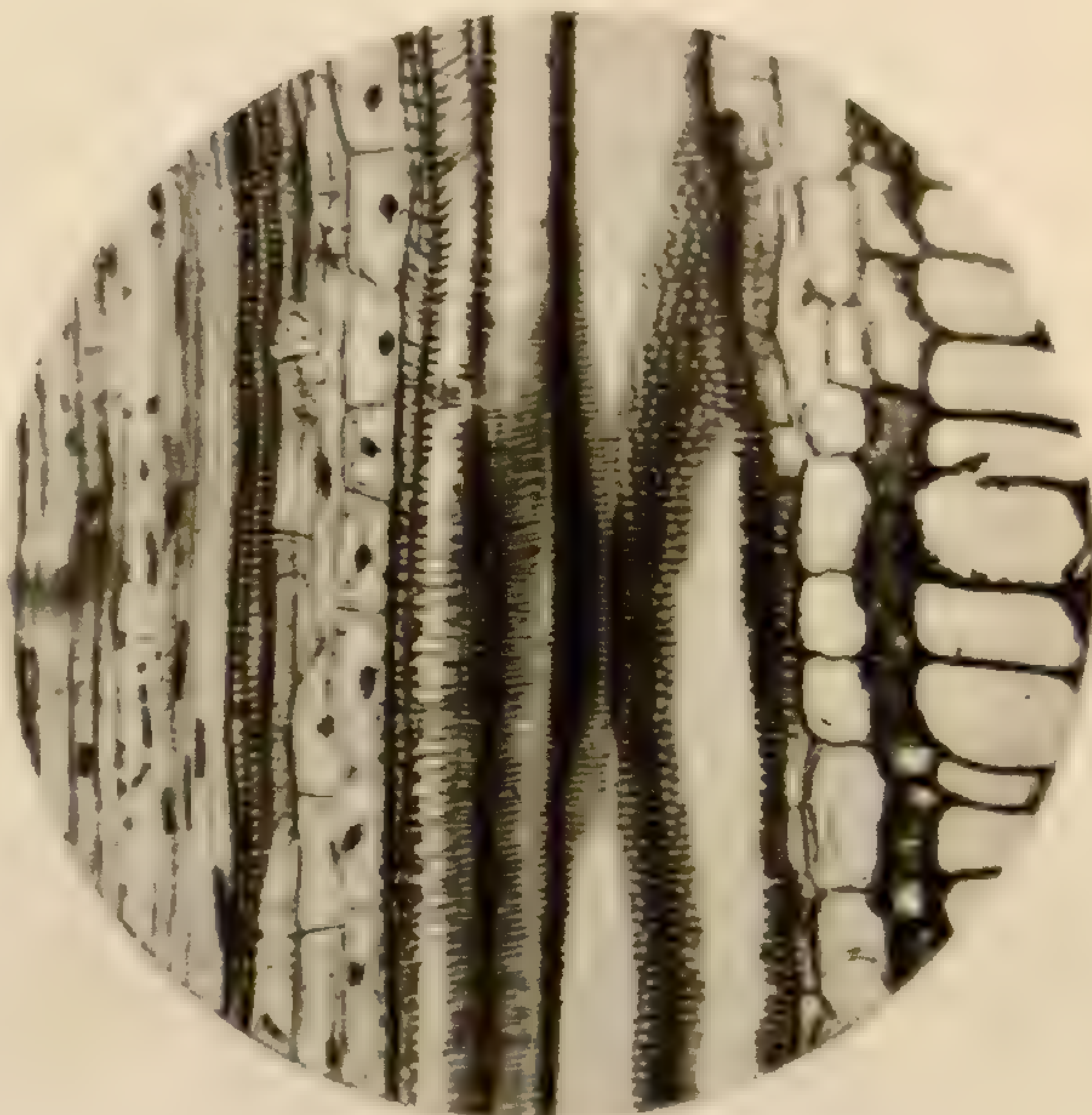
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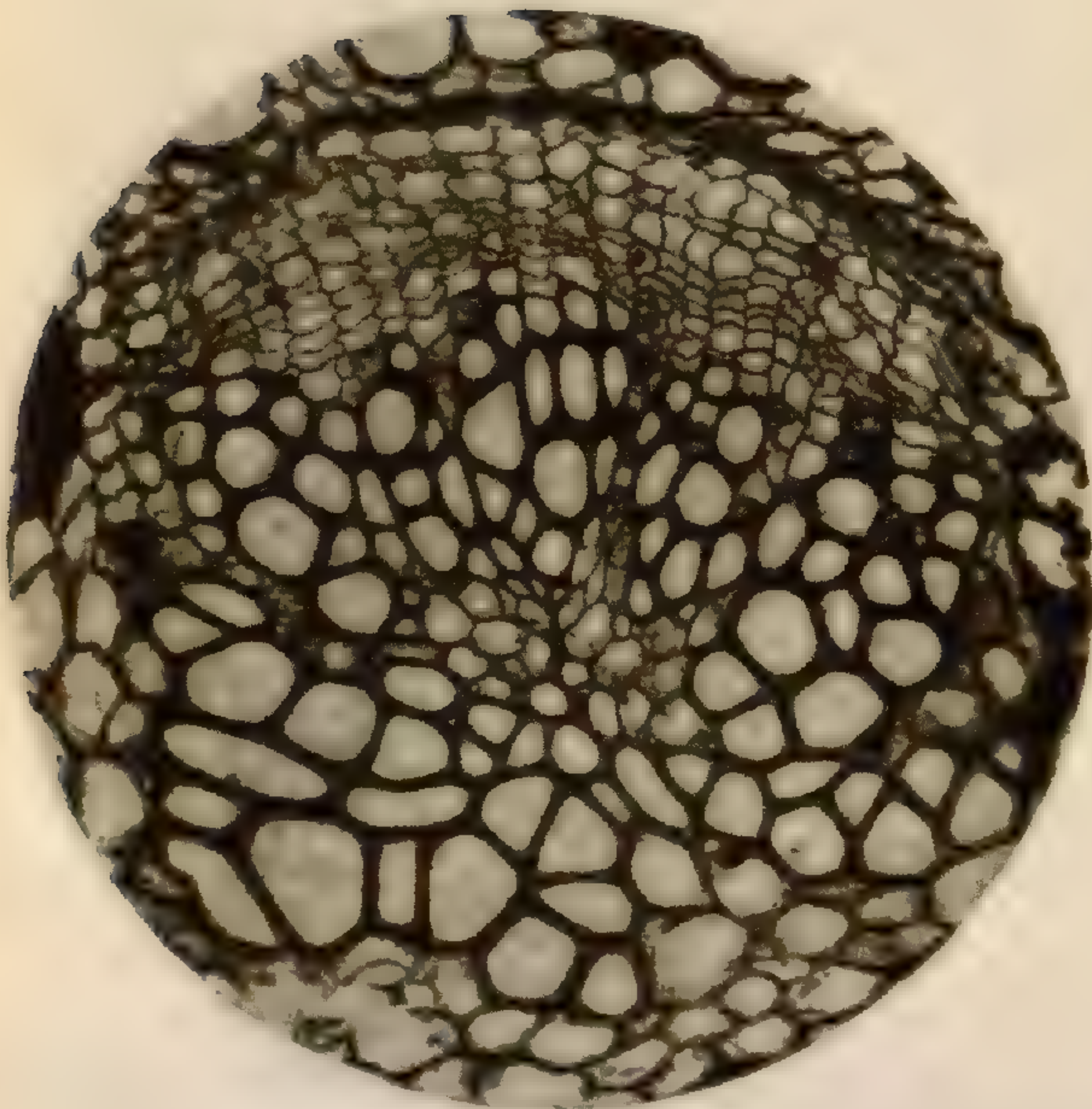
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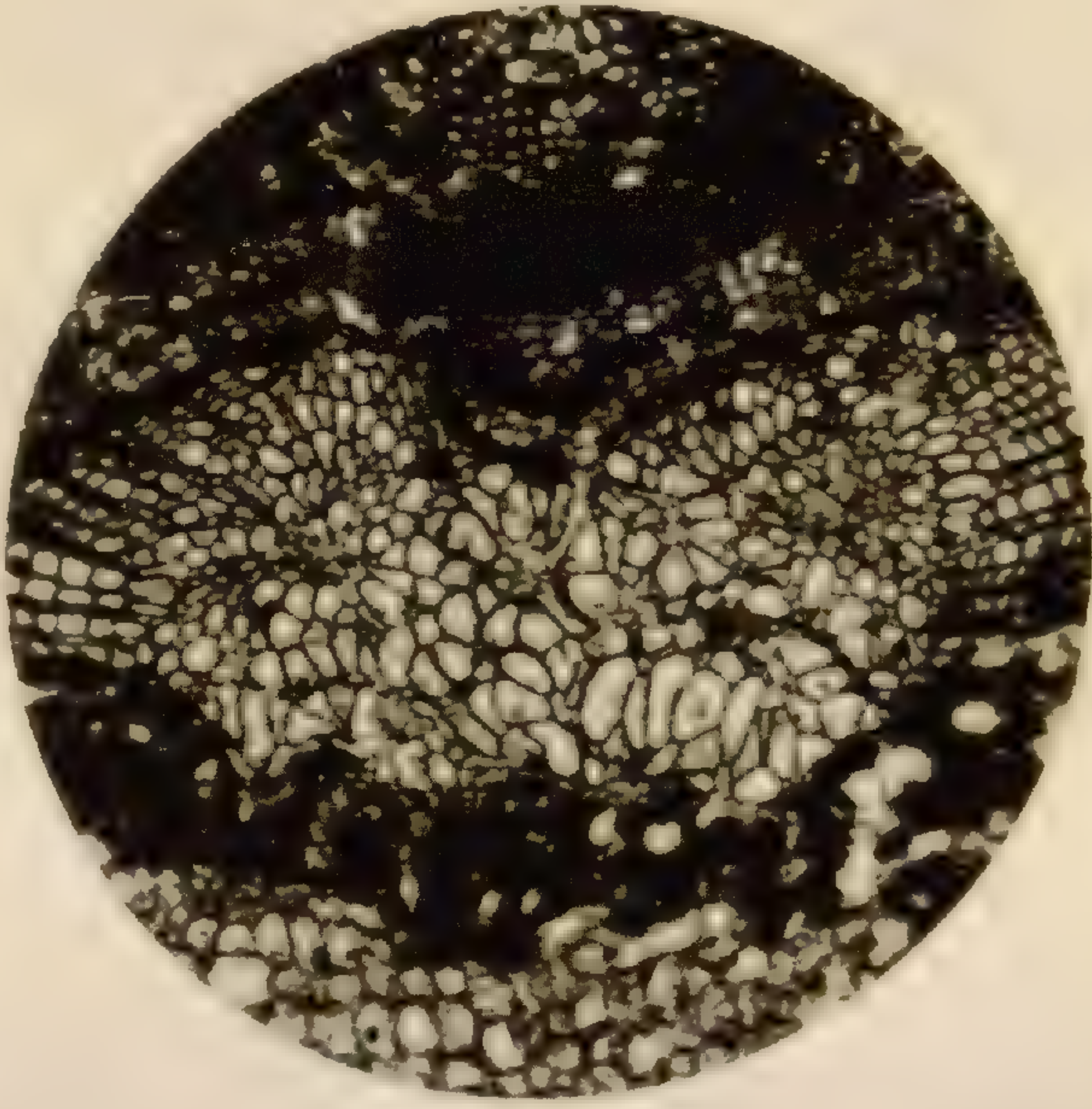
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6

CONCURRENT OXIDATION AND REDUCTION BY ROOTS¹

OSWALD SCHREINER AND M. X. SULLIVAN

EHRlich (1), whose results have been verified by others, has shown that oxidation and reduction processes may exist side by side in the animal organism. According to him the functioning protoplasm can oxidize or reduce by means of its oxygen saturated or unsaturated compounds, respectively. Since the difference in metabolism between plants and animals is one of degree only, it is to be expected that the plant cell likewise should exhibit both oxidizing and reducing powers, as has been found to be the case (2). Oxidation has been more extensively studied on account of its more readily recognized significance in life functions. Reduction, however, is probably just as important as oxidation in the economy of the living cell, and is probably just as good an index of life activity. It is most likely that in the living cell oxidation and reduction alternate in quick succession, as DRECHSEL (3-5) has shown to be the case in certain oxidations outside the living body. It is probable that in this continual oxidation and reduction protoplasm suffers no change in its essential properties and thus preserves its identity.

The literature dealing with the oxidizing power of plant juices is voluminous. Within recent years our knowledge of processes going on within the plant has been greatly enlarged by the studies which have been made on the oxidizing enzymes. This work has been comprehensively summarized by CZAPEK (6), BACH (7), KASTLE (8), and CLARK (38).

The study of the oxidizing power of the plant roots in solution cultures, on the other hand, has received less attention. MOLISCH (9) appears to have been the first to demonstrate the oxidizing power of intact roots. He found that the root secretion was

¹ Contribution from the Laboratory of Soil Fertility Investigations. Published by permission of the Secretary of Agriculture.

capable of oxidizing various organic substances such as guaiacol, pyrogallol, and gallic acid. His work showed that there was considerable active secretion on the surface of growing roots and that this secretion had definite powers to effect changes in organic substances. CZAPEK (10) repeated some of the investigations made by MOLISCH and raised some doubt as to the correctness of MOLISCH's conclusions. The fact that roots have oxidizing powers, as set forth by MOLISCH, has been well corroborated, however, by the investigations of RACIBORSKI (11), who used a number of reagents and widely different plants. He did not find a phanerogam, the roots of which did not have the property of extracellular oxidation. Great differences, however, existed between the oxidative powers of different plants.

Two classes of substances have been found useful in showing the oxidizing power of roots in solution culture. The first class comprises certain soluble chromogens which yield upon oxidation insoluble compounds mainly deposited upon the surface of the roots. The second class of chromogens consists of certain substances which give soluble coloring matter as the result of the oxidizing action of the roots, shown by the change from a colorless to a colored compound or by a change from one color to another which is distinctly different. Compounds belonging to the first class are alpha-naphthylamine, benzidine, vanillin, vanillic acid, and esculin. The second class of chromogens is in many respects more useful for oxidation studies, because the intensity of the color and hence the amount of oxidation can be quantitatively expressed. Among these substances are phenolphthalein, aloin, and leucorosolic acid.

When organic substances like alpha-naphthylamine and benzidine in solution of 10 p.p.m. and 5 p.p.m., respectively, are used, the colors due to oxidation are shown on the root. The most marked oxidation is shown by a narrow but very distinct band of color just back of the root cap. Then comes a practically colorless zone and then a broad colored zone, the color becoming less intense toward the upper part of the root. When a 0.04 per cent solution of aloin is used, a diffusion zone of color is at first formed close to the root, but in the course of a few hours the solution, as a

whole, becomes a cherry red, which varies in depth according to the amount of oxidation.

Reduction by roots has been studied but little. Reduction by the tissues of animals and by micro-organisms, on the other hand, has been extensively studied (2). The reagents used to indicate the reducing power of tissue are chromogens, which on reduction by abstraction of oxygen or by the addition of hydrogen yield a leuco-base, such as alizarin blue, indophenol blue, lacmus, methylene blue, indigo carmine, rosanilin, gentian violet; nitrates which are reduced to nitrites; sodium selenite and tellurite, which are reduced to metallic selenium and tellurium; sulphur, which is converted to hydrogen sulphide.

To show reduction we have tried various reagents and have found sodium selenite to be the best medium at our command. The selenite used was sodium selenite Merck and commercial sodium selenite Merck, the latter for the most part. Solutions of 0.25 per cent were first used. The solution reacted alkaline to litmus and phenolphthalein and was toxic to the seedling. When neutralized with hydrochloric acid, however, the toxicity of the selenite was greatly lessened. When seedlings were grown in the sodium selenite solution made neutral to phenolphthalein and of a strength of 0.125 to 0.25 per cent, the parenchyma cells of the ends of the root next to the cap were colored pink in a few hours by the deposit of selenium. The points of emergence of the secondary roots were often colored in the case of the older seedlings. After a lapse of several hours the whole root became somewhat pinkish. In solution of sodium selenite made $n/500$ acid by hydrochloric acid, the deposit of selenium at the tip of the root was very marked. In alkaline solution the reduction was very little. In short, reduction is more marked in slightly acid solutions. Oxidation, on the other hand, is stronger in slightly alkaline solutions.

As judged by the quickness with which the deposit of selenium is made on the root and the extent and intensity of the deposit, the reducing power increases from the time of germination to the sixth or eighth day and then decreases. It is still present in seedlings thirteen days old, the oldest seedling examined. The oxidative power of the wheat seedling, on the other hand, as judged by the

oxidation of aloin, is less in the young seedling and increases with age.

The relative oxidation was determined by placing the seedlings in culture bottles, 10 seedlings to a bottle, with the roots in the aloin solution made by dissolving 400 milligrams in one liter of pure distilled water. In 20 hours the depth of color produced by the red oxidation product was measured in the colorimeter. Taking the reading for the 12-day seedling as 100, the relative oxidation of the 8-day seedling was 81; of the 5-day seedling 48.

Oxidation of aloin by roots is greater in darkness than in light, the relation being in three separate tests with 4, 6, and 9-day seedlings, 100 in the darkness to 75, 70, and 71, respectively.

Nitrates and phosphates increase the oxidizing power of the wheat roots, while potassium salts, especially potassium iodide, decrease it.

TABLE I
EFFECT OF SALTS ON OXIDATION OF ALOIN BY ROOTS

			Relative oxidation
Control in pure distilled water.....			100
Sodium nitrate.....	50 p.p.m.	NH ₃	135
Potassium sulphate.....	50 p.p.m.	K ₂ O	42
Acid calcium phosphate.....	50 p.p.m.	P ₂ O ₅	117
Sodium nitrate.....	50 p.p.m.	NH ₃ , K ₂ O, P ₂ O ₅	100
Potassium sulphate.....			
Acid calcium phosphate.....			
Potassium chloride.....	50 p.p.m.	KCl	38
Potassium iodide.....	50 p.p.m.	KI	20
Iodine.....	50 p.p.m.	I	16

In the experiment given in table I, the seedlings were started germinating January 4, and were put into the nutrient solutions January 10. On January 14 the aloin was placed in the solution, and on January 15 the oxidation readings were made.

The accelerating effect on oxidation of a sodium nitrate solution containing the equivalent of 50 p.p.m. of NH₃ and the retarding effect of potassium salts equivalent to 50 p.p.m. K₂O is shown likewise in the case of plants grown in darkness. In this case the plants 6 days old were put into the salt solutions containing 0.04 per cent of aloin, and the experiment continued for 24 hours, when

the depth of the red oxidation product was measured in the colorimeter with the oxidation products of plants growing in carbon-treated water plus aloin as a control.

TABLE II

RELATIVE OXIDATION OF ALOIN BY ROOTS IN DARKNESS AND IN LIGHT

	In darkness	In light
Control.....	100	70
Sodium nitrate.....	150	105
Potassium sulphate.....	70	47
Potassium chloride.....	91	60
Potassium iodide.....	66	37

Since BIELECKI (12) has shown that nitrates of potassium, ammonium, and calcium added to a solution of peroxidase lead to its passing through a dialyzer in amounts proportionate to the amount of salt added, it may be that the nitrates increase the oxidizing activity of the wheat roots by allowing more of the oxidizing substance to pass into the medium. With alcoholic guaiac as an indicator, we have found a strong peroxidase reaction in the water in which the seedling roots had grown for 24 hours, and a stronger reaction in sodium nitrate solution in which plants have grown the same length of time. This peroxidase reaction does not occur if the culture water is boiled.

The observable action of salts on the reducing action is variable on account of lack of precision of method, though, as a rule, sodium nitrate equivalent to 50 p.p.m. NH_3 gives the quickest and heaviest deposit at the root tip, while potassium salts give the heaviest deposit on the rest of the root. The potassium salts which retard oxidation have little effect on reduction. Thus a potassium iodide solution containing 14.5 p.p.m. K_2O practically inhibited the oxidation of aloin by the roots of 5-day old wheat seedlings, while allowing good reduction of sodium selenite. It would seem, then, that reduction and oxidation may be independent of each other.

Attempts were made to show simultaneous oxidation and reduction by placing the seedlings with the roots in mixtures of sodium selenite and aloin, benzidine, and alpha-naphthylamine, respectively. In mixtures of sodium selenite and alpha-naphthylamine,

the two deposits of color on the roots were so nearly alike that it was difficult to tell whether selenium had been deposited or not in connection with oxynaphthylamine. In solution of benzidine, 5 p.p.m., the roots as a whole had a blue-black appearance, and a heavy ring appeared just back of the root cap. In the same strength of benzidine plus 0.25 per cent sodium selenite, *n*/1000 acid to phenolphthalein, the black oxidation ring at the root tip still appeared, but the roots, as a whole, were pink from the deposited selenium. In 0.04 per cent aloin and 0.15 per cent sodium selenite made *n*/500 acid, some oxidation of the aloin solution occurred and a good reduction of selenite. In aloin and sodium selenite *n*/1000 acid, there was strong oxidation and slight reduction.

The experiments show that it is possible to have oxidation and reduction by the same roots in the same solution. A slightly acid reaction is favorable to reduction, a slightly alkaline reaction favorable to oxidation. Between these acid and alkali limits both processes are demonstrable as occurring side by side.

It has long been supposed that oxidation by the plant roots and plant extracts is due to the presence of oxidizing enzymes, such as the oxidase, peroxidase, and the related catalase. A good review of the literature on cellular oxidation with consideration of the relationship between the enzymes may be found in works of BACH (7) and KASTLE (8).

According to BACH, the oxidase is a mixture of peroxidase and a peroxide-forming substance. The enzymes taking part in cellular oxidation are according to him oxygenase, peroxidase, and catalase. He explains their relationship as follows: (1) In order to have at its disposition a continued source of active oxygen, the living cell produces oxygenases or bodies capable of fixing atmospheric oxygen with the intermediary formation of peroxides; (2) the peroxides thus formed are activated by the peroxidase in the way that hydrogen peroxide is activated by ferrous sulphate; the system peroxidase-peroxide effects the oxidation of substances serving as aliments to the cell, substances which are oxidized with difficulty; (3) in cases which are particularly favorable to the formation of peroxide, excess of which might be injurious to the

cell, the cell generates a third ferment, catalase, which decomposes the peroxide with the liberation of molecular oxygen.

According to MOORE and WHITLEY (13), there is little evidence of the existence of BACH's oxygenase. These workers believe that all juices showing oxidizing properties possess one type of ferment which, since it acts only in the presence of either naturally occurring or artificial peroxide, may be styled a peroxidase. According to them there is no proof of the existence of any other type of enzyme engaged in oxidation processes.

In regard to cellular oxidation, it must be said that nothing absolutely certain is known regarding the composition or nature of the oxidizing substances in plants and the chemistry of the oxidizing bodies is uncertain. Apart from their destruction by heat and by poisons, little is known concerning their enzymotic nature. They do not seem to act as oxygen carriers in the sense of being able to transfer large amounts of oxygen from the air to the oxidizable substance, since the amount of oxidation is increased only slightly by an increase in the amount of oxygen present. Thus the relative oxidation by the roots of plants growing 4 hours in an atmosphere of pure oxygen and of air, respectively, was 100 and 80. The relative oxidation by plants in air and in a partial vacuum of a pressure of 23 mm. of mercury for 4 hours was 100 and 66; growing 19 hours in a partial vacuum, 100 and 74, respectively. In the partial vacuum the plant must oxidize the aloin by means of its intramolecular oxygen. In an atmosphere of carbon dioxide, oxidation was begun early, but this then stopped, and in 16 hours was a mere trace compared to the oxidation by plants growing in aloin solutions in air. Oxygen is necessary for plant oxidation, but a great increase in the amount of oxygen does not greatly increase the oxidation by plants.

Many, if not all, of the oxidations produced by the so-called enzymes can be brought about by non-enzymotic bodies, both organic and inorganic, as first shown by SCHÖNBEIN (14). Organic bodies like benzaldehyde, benzoyl peroxide, succinyl peroxide, pyrogalllic acid, and quinone behave like an oxidase, as do peroxides and other salts of inorganic bases such as iron, lead, manganese, etc.

SPITZER (15) attributes the oxidizing power of animal tissue to the nucleoproteid they contain, the oxidizing power of the nucleoproteid being due to the combined iron they contain. In the absence of sufficient oxygen the same nucleoproteid acts as a reducing agent. BERTRAND (16, 17) showed that the oxidizing power of laccase from *Rhus vernicifera* is associated with the presence of manganese, and that laccase of alfalfa, which is poor in manganese, is inactive toward hydroquinone (18). The mixture of a trace of manganese salt and alfalfa laccase had strong oxygen-carrying power where either constituent alone had very little. Other metals such as iron, aluminum, cerium, zinc, copper, calcium, magnesium, and potassium did not increase the oxidizing power of laccase. BERTRAND showed that manganese salts which are easily hydrolyzable are most efficient oxygen carriers. He considered the active oxidase as special combinations of manganese and an acid radical, the latter probably of a proteid nature and partaking of the properties of a ferment. The manganese would be the really active element of the oxidase, while the acid radical would give the ferment the other properties such as solubility and sensitiveness to heat.

According to REY-PAILHADE (19), the reducing ferment which he found in plants, and which he has described under the name "philothion," possesses the properties of the acid albuminoid radical of the oxidases.

In connection with BERTRAND's conception of the action of manganese and our study of the oxidation action of wheat roots, it is interesting to note that manganese has been found by MAUMENÉ (20) in many plants, among them wheat, as a salt of an organic acid. PICHARD (21) and GÖSSL (22) found manganese widespread in plants and animals. On the other hand, VADAM (23) found no manganese in the oxidase of hellebore, but did find iron; SARTHOU (24) found only calcium, iron, and sodium in the oxidase of *Schinus molle*; while DE STOECKLIN (25) could not find manganese in the ash of the oxidase from horseradish. BACH (26) believes he has obtained from molds an active oxidase which is entirely free from iron or manganese. VAN DER HAAR (27), however, doubts the validity of BACH's conclusion as regards the absence of manganese. EULER and BOLIN (28) found that laccase from

alfalfa previously studied by BERTRAND consisted of the neutral salts, mainly calcium, of certain polybasic organic acids, among which glycollic, mesoxalic, citric, malic, and probably glyoxylic acids have been determined.

Numerous inorganic compounds will change tincture of guaiac blue. Among these SCHÖNBEIN (29) mentions the oxides of the noble metals, the so-called superoxides, saltpeter, chromic acid, permanganic acid, etc., lead peroxide, bromine, chlorine, etc. ALSBERG (30) has shown that many salts have the power to change guaiac to a blue oxidation product either directly or with the addition of hydrogen peroxide. MARTINAND (31) finds that oxides of alkalies and alkaline earths which can form peroxides and percarbonates fix oxygen of the air in an active form, and form bodies which give reactions like organic oxidases. Salts of the oxides of metals possessing several degrees of oxidation give the oxidase reaction in their maximum oxidation. The oxidation was retarded by certain salts and especially by traces of sulphuric acid. WOLFF (32) found that colloidal ferrocyanide of iron exerted in certain oxidations a catalytic effect similar to that of natural peroxidases. According to WOLFF and DE STOECKLIN (33), ferrocyanides and sulphocyanates of iron can produce oxidations which can be effected by natural peroxidases, each producing specific oxidations not characteristic of the other. DE STOECKLIN (34) later found that tannate of iron in the presence of hydrogen peroxide can bring about oxidation of such compounds as generally resist the action of any natural peroxidases now known. Among the substances were phenols, cresol, thymol, anisol, carvacrol, guaicol, pyrogallol, eugenol, isoeugenol, and tyrosine.

In work with aloin, we found that a solution of ferric chloride containing 3 p.p.m. Fe gave good oxidation of aloin. Ferrous chloride, even in solutions containing 25 p.p.m. Fe, did not oxidize aloin without the addition of hydrogen peroxide. With the addition of hydrogen peroxide, 1 p.p.m. Fe as FeSO_4 strongly oxidized the aloin. Other salts which have a direct oxidizing action on aloin are manganese dioxide, calcium oxide and carbonate, and magnesium oxide. Aluminum sulphate and chloride in 5 p.p.m. solution oxidized the aloin with the addition of hydrogen per-

oxide. Sodium and potassium hydrate oxidized the aloin slowly. Copper sulphate plus sodium chloride oxidized aloin solutions immediately. On the organic side, benzaldehyde, quinone, piperidine, atropine, etc., oxidize aloin solutions readily.

From what has been said, it can be seen that there is a strong similarity between the oxidizing action of wheat roots and catalyzers like inorganic salts and benzaldehyde and quinone. Probably the similarity is one of analogy only, the methods of oxidations being but different modes of oxygen transference to easily oxidizable bodies.

KASTLE and LOEVENHART (35) concluded that the so-called oxidizing ferment of the potato is not a true enzyme, but is an organic peroxide. They believe that the oxidation phenomena occurring in plants, and probably also in animals, can be satisfactorily explained upon the supposition that the readily autoxidizable substances which they contain are oxidized to the peroxide condition by molecular oxygen, and that the peroxides thus formed in turn give up part of their oxygen to other less oxidizable substances present in the cell. In other words, the process of rendering oxygen active by the living cell is probably brought about in essentially the same way that this is accomplished by phosphorus, benzaldehyde, and other oxygen carriers.

In regard to reduction by the living cell likewise, uncertainty exists as to whether it is brought about by a true enzyme or by non-enzymotic bodies. HEFFTER (36) has given this question much attention and has come to the conclusion that the reducing activities of organisms are not due to enzymes. As in the case of oxidation, reduction processes comparable to those of the living root may be brought about by purely chemical means, as we have previously shown (2).

As regards oxidation and reduction, it may be said that oxidative bodies may be extracted from the plant roots by suitable means. No body which would reduce sodium selenite in the cold could be extracted, however, although the water extracts of the seedlings reduce the selenite on heating. Thus it seems that the reduction of the selenite by the wheat roots is due to the metabolic

activities of the roots *per se*, and is probably due to the presence of some unsaturated compounds comparable to unsaturated fatty acids, dextrose, etc., which are readily oxidized in contact with air, or to substances like organic hydroxyacids and their salts which possess a slight reducing action.

In regard to the significance of the oxidation and reduction in roots, we may say that whatever increases the development of the plant increases oxidation by the roots, and contrariwise, whatever decreases oxidation by the roots decreases the growth of the plant. In short, oxidation is closely connected with the metabolic activities of the roots. It has been shown (37) that in extracts from productive soils oxidation by roots was strong, and in extracts of certain poor soils the oxidation was little, so that from a soil-fertility standpoint oxidation by roots has considerable interest. Oxidation is due undoubtedly to bodies capable of fixing atmospheric oxygen in an active form, perhaps as peroxides, which secondarily oxidize bodies by the transfer of active oxygen to them. Reduction seems to be connected with the inner metabolism of the plant, and is probably brought about by non-enzymotic compounds analogous to the organic hydroxyacids and their salts, which have a reducing action easily demonstrable by their changing of ferric iron to ferrous iron, or to compounds unsaturated in respect to oxygen, which by their avidity for oxygen reduce the oxygen-containing compounds they come in contact with. Oxidation processes are weak in the young seedling, but increase in strength as the seedling grows. Reduction processes, on the other hand, are predominant in the early stages of the seedling's growth, but are less manifest as the seedling develops and oxidation becomes predominant. In certain stages the two processes occur together and can be made manifest either independently or concurrently. Reduction seems to be mostly intracellular. Oxidation, on the other hand, is manifested strongly extracellularly, and seems to be by far the more prominent property of the plant root.

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THE DESERT LICHENS OF RENO, NEVADA

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Reno lies at the eastern foot of the Sierra Nevada Mountains, some 15 miles from the Nevada-California boundary line, at an altitude of 4500 feet. It is built on a level tract known as the Truckee Meadows, through which flows the Truckee River. Mountains hem in this grassy valley on every side. Peavine Peak, lying northwest of the city, rises from Reno itself to a height of 8270 feet, while a little farther away and off to the southwest stands Mount Rose, with an altitude of 10,800 feet. To the north and east stretches a rolling plateau, a part of the Great Interior Basin, ridged by numerous parallel mountain ranges between which are a few streams during the rainy season and many sinks or drainage basins without outlet.

The average precipitation at Reno, as determined by observations at the University of Nevada over a period of 17 years, is 8.21 inches. A large part of this falls as snow during the winter months, or as early spring rains. The summer is hot and dry, very light showers occurring rarely. Late in the autumn light rains fall occasionally. During the entire year the diurnal changes of temperature, as in all desert regions, are very great. In winter the days are generally clear and sunny, the temperature dropping below freezing, or in some years even sometimes as low as -15° F. at night. Throughout the year strong drying winds from the west or north are very frequent, though these same west winds also bring what little rain there is. But usually they have lost their moisture in crossing the Sierras and are drying winds in Nevada. The spring is late and backward, killing frosts often occurring the last of May, and frost may occur in midsummer.

On the desert plateau proper there are no trees, except on the mountains above 6000 feet, the chief woody plants being sage brush, an *Ephedra* (Indian tea), *Grayia spinosa* (bud sage), *Emplectocladus Andersoni* (wild peach), *Purshia Kunzia* (bitter brush),

and perhaps a few other insignificant shrubs. On the mountain slopes and in the cañons above 6000 feet are found scattering clumps of *Pinus ponderosa* and *Juniperus occidentalis utahensis*, the latter sometimes forming real groves; while species of *Cercocarpus*, *Amelanchier*, and *Ceanothus* form shrubby patches 1-2 feet high, or become scraggly scattered bushes, or even trees 6-10 feet in height.

The region studied since October 1909 extends from the university campus in the city of Reno north and west a distance of 12 miles, and north and northeast about 6 miles. This district rises from 4500 feet to an altitude of over 8000 feet, the exposed rocks being mainly andesite and rhyolite.

At 5000 feet and upward lichens are, in general, exceedingly abundant on all outcropping ledges, stone pinnacles, or cliffs, as well as on the loose rocks which lie scattered about or piled in excessive quantities everywhere; but the few trees and the shrubs carry very few or no lichens. On the slopes of both Peavine and Mt. Rose I have vainly scrutinized the trunks and limbs of *Pinus ponderosa* for lichens. The trees were actually as bare as a new and freshly painted hitching post. The same condition is true of *Juniperus* out on the desert, 6 miles northeast of Reno, but 12 or 15 miles away, where there are belts of uncut juniper, *Letharia vulpina* is abundant upon it.

Before entering into a further discussion of the lichen flora of this region and the conditions which control it, let us examine the following list, which I am satisfied includes almost every species occurring below 8000 feet in this district. On Mount Rose a number of other forms appear near the summit, but the alpine lichens of that peak will be considered in a subsequent paper, as they bear no relation to the desert flora below.

1. *VERRUCARIA FUSCELLA* (Ach.) Turn.

2. *VERRUCARIA STANFORDI* Herre.—The discovery of this species here, described from the Santa Cruz Peninsula, California, greatly extends its range and is an interesting find. In addition to the type locality, I have this species from the Inner Coast Range, the Sierra Nevada Mountains along the California-Nevada boundary line above Verdi, and from the desert near Reno.

3. *DERMATOCARPON MINIATUM* (L.) Mann.
4. *DERMATOCARPON MINIATUM COMPLICATUM* (Sw.).
5. *ENDOCARPON PUSILLUM* Hedw.

6. *Endocarpon tortuosum* Herre, n. sp.—Thallus of small or irregular foliose squamules, tortuous and nodulose, often forming a rough, thick, and very irregular indeterminate crust; sometimes the squamules are densely compacted to form a thick, almost uniform torulose crust, while the squamules are stipitate, erect, and 7 mm. or more in height. When the squamules are scattered, their lobes are much dissected, and more or less complicate, recalling *E. pulvinatum*.

Color dull brown, verging from ashy brown to a dark, almost purplish brown; more or less greenish when wet; KOH—; CaCl_2O_2 —.

Apothecia minute, immersed, the ostiolum sometimes visible with a strong lens; perithecium nearly colorless or very pale brownish; asci sub-cylindrical to saccate and top-shaped, $\frac{22.5-36}{85-135.5} \mu$, their contents copper red with I; paraphyses short, confluent, blue with I; spores 2, the upper one the larger, muriform-multilocular, the locules 4 across the spore, 10 or 12 in number the long way, at first colorless and mostly pale yellowish brown, but finally dark brown, $\frac{18-27}{45-61} \mu$; hymenial gonidia elliptical, measuring $\frac{2.75-3.3}{5.6-6.7} \mu$.

The plant is abundant 2 miles north of Reno, on shaded and relatively damp rock walls with a north or northeast exposure, at an altitude of 5000 feet. It is also frequent on cliffs in a cañon above Marmol, near the state boundary line, at an altitude of 6000 feet.

7. *MICROTHELIA METZLERI* Lahm.

8. *LECIDEA ATROBRUNNEA* (Ram.) Schaerer.—I have included under this name a large series of specimens which may represent two or three species. Some of the specimens bear a very close resemblance to *Lecidea fumosa* (Hoffm.) Ach., but do not agree in the apothecial structure. Other material is probably a new

species, but I place it here for lack of further material for comparison, and because as yet the abundant apothecia have not yielded me spores.

9. *LECIDEA TESSELATA* Floerke.

10. *LECIDEA AURICULATA DIDUCENS* Th. Fr.

11. *LECIDEA SCOTOPHOLIS* (Tuck.) Herre.—A doubt is cast upon this determination because of the small spores. A specimen from California, determined by TUCKERMAN, gives spores $\frac{3-5}{8-11} \mu$,

while the Reno specimens have spores measuring but $\frac{3.5-4}{5.9-7.5} \mu$.

12. *Lecidea truckeei* Herre, n. sp.—Thallus indeterminate, apparently of medium-sized, rigid, leafy, thickish scales which are densely crowded, ascendant or imbricate, with entire or crenate margin. On removing a single plant it is seen to be peltate, prolonged downward into a stout irregular stem, and with a broad top (4-10 mm. wide) of imbricate lobules, which form the scales of the thallus as seen from above; the lobules usually concave or undulate, less often revolute, their upper surface characteristically finely reticulate and wrinkled to form convex areolae; color dull chestnut brown or yellow brown; under side of the lobules black, the stems a dusky ashen; medulla bluish or purplish with I; thallus dusky olive with KOH+CaCl₂O₂.

Apothecia small, usually numerous, black; at first very small and flat, with a thin, rather entire and slightly lighter-colored margin; becoming convex as they get larger, and more or less excluding the margin; sometimes they are conglomerate or clustered and irregular; epithecium greenish black; hypothecium brown or brownish; paraphyses confluent or agglutinate, slender, threadlike; thecium greenish pale, turning blue with I; the ventricose fertile asci are rare; spores globose, 4.66 to 7 μ in diameter.

On rhyolite, 2 miles north of Reno, at an altitude of 5000 feet, forming conspicuous patches several inches broad. Though bearing a superficial resemblance to an unusually luxuriant form of *Lecidea atro-brunnea* or some forms of *Lecidea globifera*, it is markedly different in both thallus and spores.

13. *BACIDIA TRISEPTA* (Naeg.) A. Zahlbr. (?) or *BACIDIA LECIDI- OIDES* (Anzi) (?.)—Determination uncertain for lack of properly

determined material for comparison. Spores in my specimens

measure $\frac{4.5-5.6}{11.3-14.8} \mu$.

14. RHIZOCARPON MONTAGNEI (Flot.) Koerber.

15. BIATORELLA REVERTENS (Tuck.) Herre.

16. ACAROSPORA RUFESCENS (Sm.) Th. Fr.

17. ACAROSPORA CERVINA (Pers.) Koerber.

18. ACAROSPORA SQUAMULOSA (Schrad.) Th. Fr.—Spores of Reno material are $\frac{2.2-2.33}{4-5} \mu$. This is too small for *squamulosa*,

but I cannot place our plant elsewhere.

19. ACAROSPORA THAMNINA (Tuck.) Herre.—This is a peltate plant which I place here with doubt, having no material for comparison, but it agrees fairly well with the description.

20. ACAROSPORA PELTASTICA A. Zahlbr.—Occurring in small patches amid other lichens, and rather common on the rocky débris of the desert. Hitherto known only from the deserts of southeastern California.

21. ACAROSPORA BELLA (Nyl.) Herre.

22. ACAROSPORA CHLOROPHANA (Wahlb.) Mass.

23. GYROPHORA RETICULATA (Schaer.) Th. Fr.

24. GYROPHORA HYPERBOREA (Hoffm.) Ach.

25. GYROPHORA PHAEA (Tuck.) Herre.

26. GYROPHORA EROSA (Web.) Ach.—Usually dwarfed and non-typical.

27. THYREA PULVINATA (Schaer.) Mass.—In small holes or crevices on the south and southeast face of a rhyolite cliff.

28. PECCANIA ARIZONICA (Tuck.) Herre. *Omphalaria arizonica* Tuck. *in litt.* (1884 ?).—Thallus indeterminate, dull, black, minutely fruticulose, forming sub-crustaceous pulvinate nodules, which to the naked eye appear to be composed of almost microscopic uniform granules; branches numerous, irregular, more or less knobbed, their tips often enlarged and broken up into several blunt points. Apothecia not known to me. "Spores 8, sub-globose, 0.75μ ."

A few scanty specimens were found growing on the minute quantities of earth which collects in small shallow holes on the south a face of rhyolite cliff 2 miles north of Reno.

I have a specimen collected by C. G. PRINGLE in the Santa Rita Mountains, Arizona, in 1884, and another collected by Dr. W. G. FARLOW at El Paso, Texas, and both named by TUCKERMAN *in litt.* My material from Reno agrees with both of these specimens.

All three are sterile, but on the sheet to which the one from Arizona is fastened is written the spore measurements quoted by me above, presumably copied from TUCKERMAN's findings of other and fertile material.

29. HEPPIA GUEPINI (Delis.) Nyl.

30. LECANORA GIBBOSA (Ach.) Nyl.—Part of the specimens are not at all typical and probably represent a new variety.

31. LECANORA CALCAREA (L.) Sommerf.

32. LECANORA OLIVACEA (Bagl. & Car.) Steiner (?).—The spores of my material measure but $\frac{4.6}{8.1-9.3} \mu$, while in European material they measure $\frac{5-6}{10-14} \mu$; in other respects the plant seems to agree.

33. LECANORA SAXICOLA (Poll.) Ach.—Our Nevada material is excessively variable and some forms are brought under this species with great difficulty. A brown, white-pruinose form is very common and may represent TUCKERMAN's var. *versicolor*, or it may be new.

34. LECANORA sp.—This lichen belongs to the *saxicola* group, but I am unable to determine it more closely. Intermediate between *L. saxicola* and *L. thamnoplaca*, but quite distinct from either.

35. LECANORA THAMNOPLACA Tuck.—Very abundant on loose rocks and on cliffs.

36. LECANORA MELANOPHTHALMA (DC.) Jatta.

37. LECANORA RUBINA (Vill.) Ach.

38. LECANORA RUBINA HETEROMORPHA Ach.

39. CANDELARIELLA CERINELLA (Flk.) A. Zahlbr.

40. PARMELIA GLABRA Schaerer.

41. PARMELIA EXASPERATA (Ach.) Nyl.

42. PARMELIA CONSPERSA (Ehrh.) Ach.

43. PARMELIA (?).—Too fragmentary for determination. On cold, shaded, north slopes.

44. *PARMELIA PUBESCENS* (L.) Wainio.
45. *LETHARIA VULPINA* (L.) Wainio.
46. *XANTHORIA POLYCARPUS* (Ehrh.).
47. *XANTHORIA LYCHNEUS LACINIOSA* (Schaerer).—The specimens are sterile but well marked, and grow on the north slope of a rhyolite cliff.
48. *BLASTENIA FERRUGINEA* (Huds.) Arn.
49. *CALOPLACA ELEGANS* (Link.) Th. Fr.
50. *CALOPLACA ELEGANS TRACHYPHYLLUM* Tuck.
51. *CALOPLACA MURORUM* (Hoffm.) Th. Fr.
52. *CALOPLACA CINNABARINA* (Ach.) A. Zahlbr.
53. *BUELLIA ALBO-ATRA* (Hoffm.) Th. Fr. and var. *SAXICOLA* Fries.
54. *BUELLIA TRIPHragmia* Nyl.
55. *RINODINA THYSANOTA* Tuck.
56. *RINODINA OREINA* (Ach.) Mass.
57. *PHYSCIA PULVERULENTA* (Hoffm.) Nyl.—Specimens scanty and sterile.
58. *PHYSCIA STELLARIS* (L.) Nyl.
59. *PHYSCIA TRIBACIA* (Ach.) Tuck.

It is doubtful whether one should include *Letharia vulpina* as really belonging to the desert flora. In the western Sierras it is a very abundant and conspicuous lichen, but seems hardly able to withstand the drying winds of high velocity so characteristic of the western Nevada region. On Peavine Peak, at an altitude of 7000 feet, I found two small sterile specimens growing on the butt of a scraggly *Cercocarpus*. But as already stated, where there are groves of juniper it occurs in abundance, probably because there it is sheltered from the high winds which prevent its development in more exposed situations.

Parmelia pubescens occurs at about 7500 feet on Peavine Peak, and also very sparingly on a cold north wall, where it is well sheltered from the sun, at an altitude of 5000 feet. But it is really a plant of the high Sierras and cannot be reckoned as a real factor in the desert lichen flora.

This leaves us with 57 species and subspecies which we may safely include in the flora of the desert about Reno. Of this num-

ber only three dwell on wood; *Buellia triphragmia* occurs sparingly on the trunks and limbs of sage brush, while *Xanthoria polycarpus* is rather common on the same habitat, usually near the base of the gnarled and twisted trunk, where it is well sheltered by the densely branching shrub above. *Candelariella cerinella* is best developed and most abundant on rocks, but likewise occurs on clumps of dead moss in the shadow about the base of decumbent sage brush trunks, and to some extent on the trunks themselves; but it is, properly speaking, a rock lichen.

Comparing our 55 saxicolous lichens with the 25 obtained near the Carnegie Desert Laboratory at Tucson, Arizona, we find 22 genera represented at Reno, while only 11 were collected at Tucson. Apparently but 9 species are identical in the two localities.

Three genera are especially well represented about Reno: *Lecanora* with 9 forms, *Acarospora* with 7, and *Lecidea* with 5, these three comprising over 38 per cent of the species of rock lichens of the region. If we include the highly successful *Caloplaca elegans*, we have 4 genera of the 22 which probably cover three-fourths of the rock surface devoted to lichens; while the addition of *Rinodina* and *Gyrophora* would give us at least nine-tenths of the individuals found on the desert rocks. The remaining genera are not only poor in number of species but are also poorly represented by numbers of individuals. As we pass from desert to alpine conditions, we find that *Gyrophora* becomes the dominant genus, followed by *Acarospora*, *Caloplaca*, and *Lecidea*.

The rainfall at Tucson is 13.53 inches, or 42.87 per cent greater than at Reno. Yet no species of *Lecidea* were collected at Tucson, while at Reno the genus is well represented, relatively speaking. This shows that their absence at Tucson is not due to dryness, but to other causes. It will be noted that the chief representative of the genus at Reno is the alpine or subalpine *Lecidea atrobrunnea*. In like manner we may account for the prominence of the *Lecanora rubina* group at Reno and its entire absence at Tucson by the higher altitude and prevailing low temperature for a large part of the year at Reno, these species of *Lecanora* being characteristically subalpine or alpine plants.

The coloring characteristic of the rock ledges of the desert and

cañon walls is often entirely due to lichens, and in a general way they form the only brilliant plant formations in a landscape notable for its subdued, pale, monotonous tones. Most conspicuous are *Acarospora chlorophana* and *Caloplaca elegans*, which form striking landmarks when covering great crags and rock walls. The next most conspicuous lichens are *Rinodina oreina* and *Lecanora rubina* and its allies, which often entirely cover immense boulders and northerly sloping rock walls. In places *Gyrophora erosa* and *Gyrophora phaea* may cover the rocks to the exclusion of other forms, but their dull brown shades are not at all conspicuous. *Gyrophora reticulata* is sometimes the sole occupant of northwest exposures, when its black thallus becomes quite noticeable.

Candelariella cerinella and *Acarospora bella* are perhaps the only others which would attract the attention of the casual observer, nearly all the others having a dull or somber brown or dusky hue which blends in with the general rock color.

The species of *Dermatocarpon* occur in crevices of rock walls, especially on northeastern and southeastern slopes, where they receive the maximum of protection from drying winds. The few small specimens of *Physcia* occur in the same localities, where they are very little or not at all exposed to direct sunlight. The remaining lichens, except where previously noted, occur indifferently on all sides of boulders or rock ledges, the sunniest and most arid of all possible situations, where one would hardly believe a plant could exist, being occupied by *Gyrophora phaea* and *Acarospora thamnina*. The largest and finest specimens of *Gyrophora reticulata*, as well as the best specimens of *Lecanora rubina*, are on northern or northwesterly exposures; this I attribute to the fact that these slopes are much colder, being exposed to the direct winds from the snow fields of the Sierras, and are also often covered for weeks with great snow drifts.

With the exception of *Lecanora rubina* and its allies, few of the well exposed rock lichens could fairly be called foliose. The short-lobed species of *Gyrophora* hug the rocks as closely as possible, so that they are truly crustose except when in some sheltered crevice or more than ordinarily favorable position. The quite inconspicuous and sterile thallus of *Parmelia exasperata* and *Parmelia glabra*

is usually far more closely attached to the rocks than many of the species of *Lecidea* or *Acarospora*.

In FINK's study of the Tucson lichens, he speaks of the remarkable development of black lines or spots on the upper surface of every species having a light-colored thallus. I find practically nothing of the kind on the lighter-colored species at Reno, such as *Acarospora chlorophana*, *Acarospora thamnina*, *Lecanora gibbosa*, *Buellia albo-atra*, or *Physcia stellaris*, though all but the last named occur frequently where they are exposed to the full glare of a brilliant sun set in a cloudless sky for ten or twelve hours daily during most of the year. I do find some such dark spots on *Rinodina oreina*, but not any more, if as many, as occur on it in regions elsewhere with a rainfall of 20 inches. *Acarospora thamnina* and other sterile light-colored lichens are often blotched with dark spots simulating apothecia, but a section shows them to be parasitic fungi.

Certain species of *Acarospora* and *Lecidea* are noticeable for the thickness and comparative luxuriance of their thallus, and for their sterility, certain forms which I can identify with difficulty or not all at being persistently sterile though of a rank vegetative growth.

In his study of the Tucson desert lichen flora, FINK takes up the question of the amount of moisture desert rock lichens may obtain from the upward passage of water through the rocks. Geologists and botanists here in Nevada do not believe that lichens obtain any appreciable amount of water from the desert rocks upon which they grow by the upward passage of moisture through the rocks. All observation goes to substantiate FINK's statement "that lichens absorb at least a large proportion of the moisture needed directly from water vapor of the atmosphere and from water falling upon them." Incomplete experiments by me show that lichens not only retain a considerable amount of moisture within their thalli even in the driest times, but that they imbibe moisture from rain with very great rapidity and in great quantity, relatively speaking.

But that the desert lichens of this region do not depend upon water obtained by capillarity is readily understood when one exam-

ines the vast numbers of loose rocks lying upon air-dry soil, yet thickly covered with lichens. This fact is impressed still more strongly when one sees the luxuriant growth of certain lichens upon the loose slabs and fragments forming the talus about cliffs; often they are some feet above the soil or outcropping rock, and lie in such a position that the hot desert air blows all about them, under as well as over; yet the lichens seem to thrive as well on these fragments as on the cliff itself. In these cases it seems plain that the only source of water for the lichens thereon is from direct precipitation and from the atmosphere.

During the summer months it is highly probable that a careful study would show that the great diurnal drop in temperature which comes in all arid regions with the advent of darkness is likewise accompanied by a deposition of moisture upon, or at least an increase in water content of, the desert lichens.

When one considers that the temperature drops 30° to 35° F. every night during the summer months, it is apparent that without any increase in the actual amount of water present there is a great increase in the percentage of moisture, and it is believed by some of us that the lichens are able to take advantage of this relative increase and absorb enough moisture to maintain their vitality during the long, hot, dry season.

Though the winters here are characterized by a comparatively low temperature, they are yet open and sunny, so that during the daylight hours they are usually quite mild. This mildness and the fact that the winter is the season when most moisture is available, especially that from melting snows, cause the lichens to have their period of most active growth during the months from November to June. Except under unusually favorable conditions, it is not likely that the Nevada desert lichens are more than able barely to keep alive during the remainder of the year.

That desert conditions are, in the main, unfavorable to the growth of lichens as a whole is shown by the limited number of genera and species represented, while a considerable number of those found are able to maintain themselves only in the most favorable spots, such as under overhanging rocks on the north side of cliffs, or deep within crevices. But that some species are per-

fectly at home in the midst of the most adverse desert conditions of excessive light and dryness is shown by the fact that almost everywhere the rocks are just as thickly covered with lichens as in other regions of greater humidity and less sunshine. The desert does not lack in number of individuals, but in number of species of lichens able to adapt themselves to its conditions.

OAKLAND, CALIFORNIA

BRIEFER ARTICLES

A CONVENIENT MICROTOME KNIFE

(WITH FIVE FIGURES)

Few people know how to sharpen a microtome knife, and those who have acquired the art usually have something else to do. The professional knife sharpener will grind out the nicks but will not produce the edge needed for paraffin cutting, and it is useless to explain what one wants, because he sharpens operating knives for the best surgeons in the city, and what is good enough for them is good enough for a botanist.

Several years ago we suggested that if manufacturers would make a clamp to hold the blade of the Gillette safety razor, its hard, even edge would doubtless be satisfactory for microtome sections, and the blades being rather cheap, it would not be necessary to sharpen them when they became dull. Numerous attempts to make a holder proved more or less unsatisfactory. Some of these discarded holders were very much like one described in the current number of *Annals of Botany*.¹ The objection to this knife is that the blade, being held between two flat pieces of steel, is not absolutely rigid. Further, such a holder clamped directly into the microtome does not place the edge of the blade in the most favorable position for cutting.

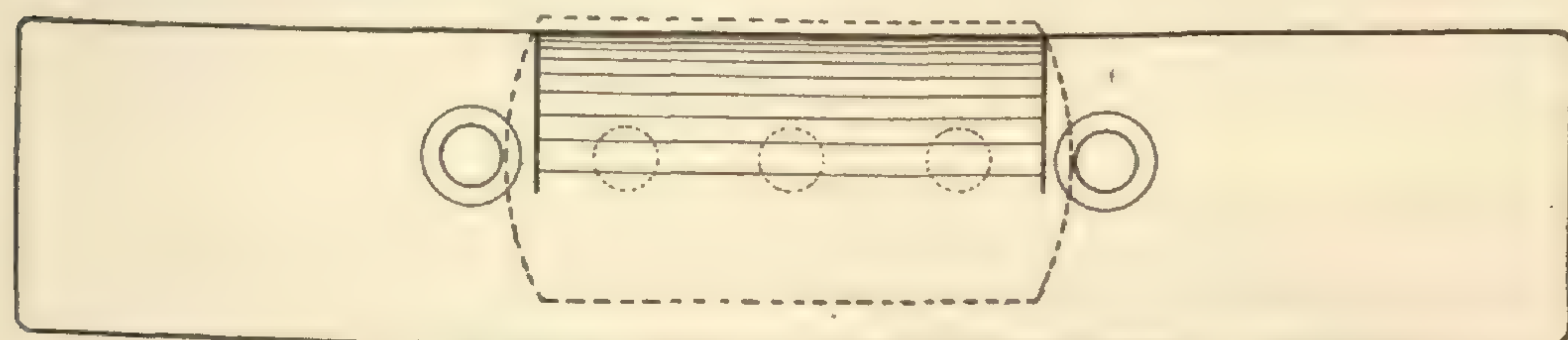
After our own efforts had failed to secure the results which we believed the cutting edge of the safety razor should produce, we prevailed upon a well-known optical company to make a sample holder, and this was fairly satisfactory, but the price (\$13) seemed practically prohibitive.

We then explained to a skilled mechanic² just what we wanted, and he made a holder which is quite satisfactory and costs only \$3. It is made of brass and can be used in either rotary or sliding microtomes; the essential features can be seen in figs. 1-5. About 13 or 14 cm. is a convenient length for the holder. The sectional views show that the two pieces are not straight, but are slightly curved, a feature which insures

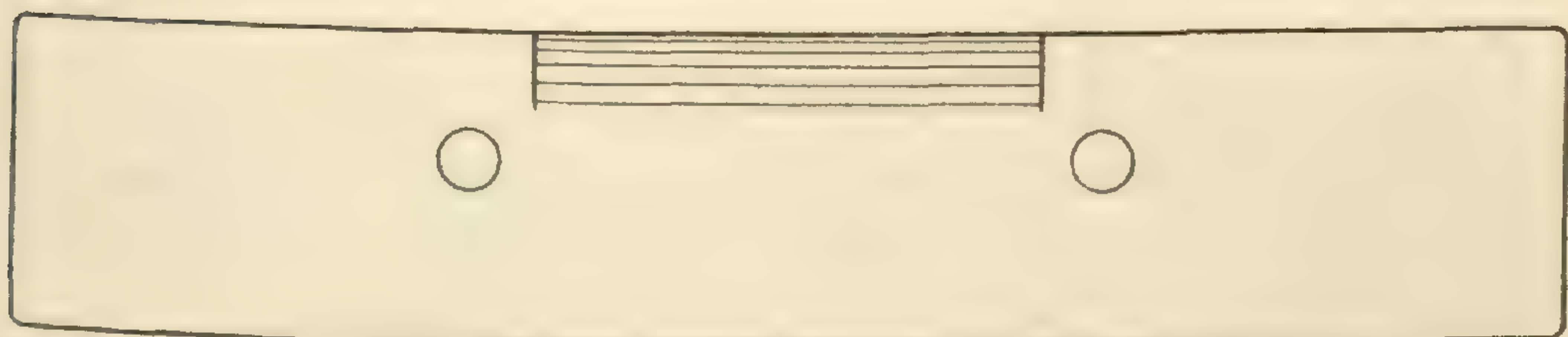
¹ BENTLEY, B. H., An arrangement for using the blades of safety razors in the microtome. *Annals of Botany* 25:273-275. 1911.

² A. W. STRICKLER, 1311 E. 57th Street, Chicago, Ill.
Botanical Gazette, vol. 51]

great rigidity, and also allows the paraffin block to clear readily. The curve is easily secured by cutting the two parts of the holder from two large brass tubes, one being about 12.5 cm. in diameter, and the other fitting as closely within it as an ocular in a microscope. The thickness should be about 3 mm.



1



2



3



4



5

FIGS. 1-5.—Fig. 1, back view; fig. 2, front view (toward the paraffin block); fig. 3, end view; fig. 4, sectional view at the middle; fig. 5, sectional view at the screws, which are represented by the double circles in fig. 1, and by the single circles in fig. 2.

It is neither necessary nor desirable to have pins fitting the three holes in the knife, since they add nothing to the rigidity and even interfere with the insertion and adjustment of the blade. The binding screws should be as close as possible to the blade, and not at the ends of the holder, as shown in the form described in the *Annals of Botany*.

With the Gillette blade in this holder, we have cut smooth sections 2 and 3 μ in thickness, and have also cut large sections 2 cm. in diameter and 15 μ in thickness, even such refractory objects as the strobili of *Isoetes* and *Selaginella* cutting as smoothly as with a first-class microtome knife in perfect condition.

In general, the blade should project only far enough to allow the paraffin block to clear. Naturally, the blade might project a little farther in case of thin delicate sections than with thick hard ones, but a little experience will accustom one to the use of such a knife, and the luxury of having at all times a fresh keen cutting edge will be appreciated by all who have known the drudgery demanded by the microtome knives in general use.—CHARLES J. CHAMBERLAIN, *The University of Chicago*.

ADDITIONS TO THE GRASSES OF CUBA

Since the publication of the *Catalogue of the grasses of Cuba*,³ several additional species of grasses have been contributed to the National Herbarium by Brother LEÓN of the Colegio de la Salle, Habana. The following is a list of these:

MANISURIS EXALTATA (L. f.) Kuntze, Rev. Gen. Pl. 2:779. 1891.

Stegosauria exaltata Nash, N. Amer. Fl. 17:84. 1909.

This species is retained provisionally in *Manisuris* until the genera of Andropogoneae are more carefully examined.

Sancti Spiritus, León 847.

ANDROPOGON SQUARROSUS L. f. Suppl. 433. 1781.

Habana, León 1581. Introduced.

ANDROPOGON CARICOSUS L. Sp. Pl. ed. 2. 2:1480. 1763.

Guanabacoa, León 2013. Introduced.

Sorghastrum agrostoides (Speg.).

Andropogon agrostoides Speg. Pl. Nov. Nonnul. Amer. Austr. Dec. 2:27. 1883.

Sancti Spiritus, León 895.

PASPALUM BLEPHAROPHYLLUM Nash, in Small Fl. Southeast. U.S. 71. 1903.

Marianao, León, 779.

PASPALUM HELLERI Nash, Bull. Torrey Club 30:376. 1903.

Santiago de Cuba, León 951.

PASPALUM MONOSTACHYUM (H. B. K.) Vasey, in Chapm. Fl. South. U.S. ed. 2. 665. 1889.

Zaza de Tunas, Santa Clara, León 947. The spikelets are smaller than in the typical form.

³ HITCHCOCK, A. S., Contr. Nat. Herb. 12:183-258. 1909.

Paspalum Leoninum Chase, sp. nov.—A low tufted perennial, with narrow leaves mostly crowded at the base, slender nearly naked culms and solitary usually purplish racemes. Culms 15–35 cm. high, very slender, wiry, compressed, ascending or spreading and more or less sinuous, glabrous, the nodes ascending-pubescent; lower sheaths overlapping and keeled, glabrous or sparsely pubescent on the scarious margin and with a few stiff hairs on the auricles, usually but a single leaf about midway on the culm, the sheath with a few scattered long hairs or glabrous; ligule membranaceous, about 0.5 mm. long; blades flat or somewhat involute from a folded base narrower than the summit of the sheath, 3–7 cm. long, 1–2 mm. wide, more or less curled, glabrous on both surfaces or minutely puberulent on the upper, a few stiff hairs on the margin and rarely on the upper surface, the blade of the uppermost leaf reduced to a mere tip; raceme 2–3.5 cm. long, slightly curved, a few long hairs at the base; spikelets solitary, on very short, flattened, scabrous pedicels, closely imbricated, almost concavo-convex, 1.3–1.5 mm. long, about 0.7 mm. wide, oval, glabrous; second glume 3-nerved, the sterile lemma with a nerve near either margin, the midnerve suppressed or apparent only at the summit; fruit nearly as large as the spikelet.

Type U.S. National Herbarium no. 618,754; collected August 30, 1909, on "Obispo hill, near Sancti Spiritus," by Brother *León* (no. 950).

This species is most nearly related to *Paspalum rupestre* Trin., from single-spiked specimens of which it may be distinguished by the more delicate culms and the more closely imbricated, glabrous spikelets, the second glume with the midnerve suppressed.

Paspalum Leoninum is named in honor of Brother LEÓN, of the Colegio de la Salle, Vedado, Habana, whose collections have added greatly to our knowledge of the grasses of Cuba.

A second collection of this species was made on the Jata Hills, Guanabacoa, September 12, 1909, *León* 949.

CENCHRUS MYOSUROIDES H. B. K. Nov. Gen. & Sp. 1:115. 1816.

Santiago de Cuba, *León* 835.

GOUINIA POLYGAMA Fourn. Mex. Pl. 2:103. 1886.

Cojimar, *León* 2014.

ARUNDO DONAX L. Sp. Pl. 81. 1753.

Marianao, *León* 1523. Escaped from cultivation.

LOLIUM TEMULENTUM ARVENSE (With.) Bab. Man. Brit. Bot. 377. 1843.

Habana, *León* 1583. Introduced.

It may be well to record here certain changes in the names of a few species of *Panicum* listed in the *Catalogue*, as shown by the recent revision of this group.⁴

Panicum aquaticum Poir. This is a synonym of *P. dichotomiflorum* Michx. The Cuban species is *P. elephantipes* Nees.

Panicum compactum Sw. = **Lasiacis compacta** (Sw.).

Panicum distantiflorum Rich. To this species was referred *Panicum utowanaeum* Scribn. (*P. Sintenisii* Nash), which proves to be a distinct species. It is represented by two specimens from Tricornia, near Habana, *Hitchcock* 141 and *Tracy* 9089.

Panicum divaricatum L. = **LASIACIS DIVARICATA** (L.) Hitchc.

Panicum Grisebachii Nash = **Lasiacis Grisebachii** (Nash).

Panicum hirtivaginum Hitchc. This species appears to be the same as *P. Ghiesbreghtii* Fourn. of Mexico.

Panicum laxum Sw. To this was referred *P. polygonatum* Schrad. which, however, proves to be distinct, and is easily recognized by its pubescent nodes, and by the lack of the swollen sterile palea which characterizes *P. laxum* and *P. pilosum*.

Panicum numidianum Lam. This species appears to be confined to the North African area and, though not well known, is sufficiently distinct from *P. barbinode* Trin. of Cuba and tropical America.

Panicum Rugellii Griseb. = **Lasiacis Rugellii** (Griseb.).

Panicum Sellovii Nees. An earlier name is *P. millegrana* Poir.

Panicum Sloanei Griseb. = **Lasiacis Sloanei** (Griseb.).

Panicum Swartzianum Hitchc. = **Lasiacis Swartziana** (Hitchc.).

To these may be added the following two corrections in genera allied to *Panicum*:

Mesosetum rottboellioides (H. B. K.) Hitchc. A comparison of the type specimens shows that the Cuban species is **Mesosetum loliiforme** (Hochst.) Chase (*Panicum loliiforme* Hochst.⁵).

Hymenachne auriculata (Willd.) Chase. The specimen mentioned, Wright 3863 in part, is *H. patula* Fourn.⁶—A. S. HITCHCOCK, U.S. Department of Agriculture, Washington, D.C.

⁴ HITCHCOCK and CHASE, Contr. Nat. Herb. 15:1-396. 1910.

⁵ Steud. Syn. Pl. Glum. 1:56. 1854.

⁶ Mex. Pl. 2:37. 1886.

CURRENT LITERATURE

BOOK REVIEWS

Fertilization

The problem of fertilization has been studied chiefly by morphologists, who have limited themselves rather strictly to the structures concerned, and consequently a book by a prominent investigator,¹ dealing primarily with the physiological aspects of the case, cannot fail to be interesting and helpful. While the physiological standpoint is everywhere in evidence, the morphology is fairly presented, and the general conclusions, based upon both physiology and morphology, are suggestive.

Fortunately, NĚMEC does not confine himself to fertilization as usually defined, but devotes a large share of his attention to nuclear and cell phenomena in vegetative tissues, where he believes such phenomena may be of value in interpreting the process of fertilization. In this connection he discusses multinucleate cells, fusions in such cells, karyomere-formation, and the effect of chloral hydrate and chloroform upon cells and nuclei. Some attention is given to the behavior of nuclei in wound tissue, and to the influence of plasmolysis upon nuclear and cell division. Interesting chapters deal with the development of the chromosome and reconstruction of the nucleus, and with the influence of external factors upon the form of the chromosome. There is also a chapter upon the microchemistry of the nucleus and mitotic figure. These are the principal features of the first, or special part of the book.

The second, or general part, may seem to cover the whole field of cytology, but a glance at the chapter headings shows that the wide range of matter is pertinent and emphasizes the breadth of the subject. The headings are: the persistence and individuality of the chromosome; the relation between the size of nuclei and cells; the position of the nucleus; vegetative and sexual nuclear fusions; the reduction of chromosomes; the significance of chromosome numbers in alternation of generations; the nucleus as the bearer of hereditary characters; the nature of fertilization; and the individuality of the cell in the tissue.

Space would hardly permit a discussion of all these fundamental problems, but a mere statement of NĚMEC's position may be of interest. He believes that the hypothesis of the individuality of the chromosome offers the best explanation of the known facts, and suggests that the individuality may yet be demonstrated, perhaps by microchemical methods. Further, the number

¹ NĚMEC, B., *Das Problem der Befruchtungsvorgänge und andere cytologische Fragen*. 8vo. pp. 532. pls. 5. figs. 119. Berlin: Gebrüder Borntraeger. 1910. M20.

of chromosomes (*ceteris paribus*) regulates the size of the nucleus and furnishes the best evidence for the individuality hypothesis. Nuclear fusion and reduction of chromosomes are regarded as important autoregulative processes which take place only under definite internal and external conditions. Although admitting that the nucleus is of great importance in transmitting hereditary characters, he does not believe that it is the sole bearer of such characters, but that this function is performed by the nucleus and cytoplasm together.

It is fortunate that physiological methods are being brought to bear upon morphological and cytological problems. The morphologist, with his limited knowledge of physiology, is necessarily one-sided in his methods and conclusions; the physiologist, with a correspondingly limited knowledge of structures and development, brings other methods and other viewpoints to the solution of the problem; and thus each corrects and stimulates the other, so that problems which either could not solve alone become possible. The strict morphologist and cytologist will find in this book much with which he cannot agree, but nevertheless he will be compelled to recognize it as a valuable contribution to the subject.—CHARLES J. CHAMBERLAIN.

Response to light

MAST² has written a thoroughly interesting book on the response of organisms to light. It consists of four parts: "Introduction and historical review" (pp. 1-57); "Experimental observations and discussions bearing on the question as to how organisms (especially those without eyes) bend or turn and move toward or from a source of stimulation" (pp. 59-235); "General considerations of reactions to light" (pp. 236-298); and "Reaction in light of different wave-lengths or colors" (pp. 304-393). A bibliography of 14 pages cites the more important literature on the subject, and frequent and excellent summaries make the main conclusions readily accessible.

The work brings together our knowledge of the response to light in plants, motile and sessile, and in animals, protozoa and metazoa. It is a consideration of response to light from the evolutionary point of view. MAST says, "the generality of the treatment of the subject of actions in organisms, including plants as well as animals, it is hoped will make the work of value to all students of nature, especially to those interested in comparative psychology, zoology, botany, and physiology."

Much of the second part is a statement of the author's own research. His work was mainly with animals, yet he has made contributions to plant response. He takes up the long discussed question as to whether directive response to light is determined by the direction of the rays or by the difference of intensity on different flanks. He uses the maize seedling with apparatus that apparently answers all the objections to former methods. His results

² MAST, S. O., Light and the behavior of organisms. 8vo. pp. xi+410. figs. 35. New York and London: John Wiley and Sons. 1911.

seem to prove conclusively that OLTMANN's intensity theory is right, and that SACHS's ray direction theory is wrong. This chapter alone is no mean contribution.

At many points the author opposes LOEB's conception of response. This is done with vigor, if not with feeling. Quotations from the summary of part II put forth some of the questions in dispute: "There is no conclusive evidence, except perhaps in animals with image-forming eyes, showing that light acts continuously as a directive stimulus, that symmetrically located sides are continuously stimulated, equally when the light intensity on them is equal, unequally when it is not, and this regulates orientation by regulating the rate of motion of the locomotor apparatus on the two sides as is demanded by the theories of DECANDOLLE, LOEB, VERWORN, DAVENPORT, and RÁDL."

"There is no conclusive evidence showing that orientation in light is ever due to tropic reaction in any organisms, if the definitions of tropisms given by LOEB, VERWORN, or RÁDL are used as criteria."

"The idea of reactions to change of intensity, however, is not original with LOEB, as is sometimes assumed. The explanations of reactions to light given by ENGELMANN, BERT, GARBER, LUBBOCK, ROMANES, DARWIN, and others, all of whom preceded LOEB, were largely founded on this idea."

The work in the main agrees with JENNINGS' results and conclusions from his extensive studies. It supports his views on trial reactions, motor reflex, physiological state, and the adaptive character of reactions.—WILLIAM CROCKER.

MINOR NOTICES

Trees and shrubs of Southern California.—Abrams³ has published the results of an extended field and herbarium study of the trees and shrubs of southern California. The territory involves about 40,000 square miles, or approximately one-fourth the area of the entire state. The author gives a careful consideration of the general physiographic and phytogeographic features of the southern portion of the state, and divides this area into three floral regions: (1) *the coastal slope*, (2) *the mountain*, and (3) *the desert*. The species of the first region are said to be "principally of Californian origin," of the second "boreal or of boreal ancestry," and of the third "endemic or migrants from the Great Basin, Sonora, or Lower California." Each floral region is divided into zones, in accordance with MERRIAM's outline, and these again are defined and characterized in more or less detail.

The body of the work bears the modest title of "Annotated catalogue of the southern California trees and shrubs." It is indeed far more than the term "catalogue" implies, since the text is provided with succinct keys to genera and species in most of the larger groups; there is also a limited amount of synonymy, copious notes, and ample citation of exsiccatae. New species

³ ABRAMS, LEROY, A phytogeographic and taxonomic study of the southern California trees and shrubs. Bull. N.Y. Bot. Gard. 6:300-485. pls. 10. 1910.

are recorded in *Lupinus* (*L. Brittoni*), *Amorpha* (*A. occidentalis*), *Ceanothus* (*C. austro-montanus*), and *Malacothamnus* (*M. Nuttallii*); and several new combinations are made. The work includes 375 recognized species, representing approximately 150 genera, distributed in 57 families. Whether or not we agree with the limitation of groups and the nomenclature in all cases is a matter of minor significance. It is a pleasure to state that the author has given us a work which will serve as an exceedingly helpful guide in studying the woody plants of southern California.—J. M. GREENMAN.

North American Flora.⁴—Volume III, part 1, contains a treatment of the Nectriaceae and Hypocreaceae by F. J. SEAVER, the Chaetomiaceae by H. L. PALLISER, and the Fimetiariaceae by D. GRIFFITHS and F. J. SEAVER. These four families are represented by 242 species which are referred to 45 genera. One new species is described in *Scoleonectria* (*S. tetraspora*), found growing on trunks of cacao in Jamaica, and four new species from eastern and central United States are added to *Chaetomium*.—J. M. GREENMAN.

Revision of Eucalyptus.—The recent issue of Volume II, part 2, continues MR. MAIDEN'S⁵ excellent revision of this genus. The present part contains descriptive matter relating to ten species and four full-page illustrations. This work can be used advantageously in conjunction with the "Forest flora of New South Wales" by the same author.—J. M. GREENMAN.

NOTES FOR STUDENTS

Cystidia of Coprinus.—BULLER⁶ has given an interesting account of his studies on the cystidia of *Coprinus atramentarius*. The lamellae of this species are very thin, broad, with parallel sides, and lie very close together. Because of their soft texture and extreme flexibility, many of them would lie very close together, or actually adhere, were it not for some kind of stay or prop for spacing them. The spores, then, which are shot off from the sterigmata could not fall down and out from the interlamellar spaces. The cystidia function as props to hold the lamellae equidistant. They are large cylindrical cells, with a slender stalk, which grow out from the subhymenium, the broad portion extending across the interlamellar space against the opposite gill surface or sometimes slightly entering it. They are $120-170 \times 20-30 \mu$, quite evenly distributed, there being about 75-100 on each square mm. of gill surface.

⁴ North American flora, Vol. III, part 1, pp. 1-88. New York Botanical Garden. December 29, 1910.

⁵ MAIDEN, J. H., A critical revision of the genus *Eucalyptus*, Vol. II, part 2, pp. 61-100, pls. 53-56. Sydney: William Applegate Gullick. 1910.

⁶ BULLER, A. H. R., The function and fate of the cystidia of *Coprinus atramentarius*, together with some general remarks on *Coprinus* fruit bodies. *Annals of Botany* 24:613-629. pls. 50, 51. 1910.

The large number of cystidia thus crossing the interlamellar spaces would themselves be a great hindrance to the escape of the spores in their fall were it not for the fact that they disappear from the area of spore discharge just prior to the maturity and discharge of the spores. The author has shown in a previous publication⁷ that in a large number of Hymenomycetes studied the spores are shot from the sterigmata to near the middle of the interlamellar space, and then fall slowly downward and out where they are caught by air currents. He also has shown that in large Coprini like *C. comatus*, where the gills are broad and lie very near each other, the maturity and discharge of the spores begins over a limited area at the lower end and edge of the gills and proceeds upward, and that this is followed by the deliquescence of the lamellae in the same succession, thus leaving a broader space for the fall of the spores. He believes this deliquescence is brought about by enzymes formed in the cells, and so applies the term "auto-digestion."

He now shows that in *C. atramentarius* the same progress of spore development, discharge, and autodigestion of the lamellae takes place, and further, that the cystidia disappear in advance of spore discharge by a similar autodigestion, the fluid content of the large cystidium perhaps being absorbed by the subhymenium, while the wall is digested. In *C. comatus* he says there are no cystidia on the sides of the gills, but the edges are provided with numerous larger, elongated cells which are crowded and many of which extend laterally, thus meeting those of adjacent gills. This broad gill margin, which is absent in *C. atramentarius*, thus serves to prop the gills apart.

In his general remarks on *Coprinus* fruit bodies, he points out that the type of gill in *Coprinus*, very thin and with parallel sides, is not so well adapted to spore escape as the thicker and more or less V-shaped gill of the mushroom (*Agaricus campestris*) type, since the overhang permits the spores to escape readily, and thus they are maturing simultaneously over the entire hymenial surface. The lamellae of the Coprini which lack this overhang mature their spores from below upward. Autodigestion removes the older portions after spore discharge and the cystidia before spore discharge, the whole series of events showing a remarkable adaptation.

He has now determined that even in the plicate Coprini there is slight autodigestion of the lower edge of the gills. The splitting of the gill from above downward probably gives an overhang here, and thus the form of the gill is ultimately more of the V-shape.

He has found cystidia as props in *C. atramentarius*, *C. narcoticus*, *C. stercorearius*, *C. fimetarius*, and *C. niveus*; while the following lack cystidia on the sides of gills but have the tumid margin: *C. comatus*, *C. sterquilinus*, and *C. plicatiloides*. Autodigestion has been observed in eight species of *Coprinus*.

In his general remarks on cystidia he states that they are unbranched. However, one genus of Thelephoraceae (*Asterostroma*) and one of Hydnaceae

⁷ BULLER, A. H. R., Researches on Fungi. pp. 287. 1909.

(*Asterodon*) are so named because of the presence of stellately branched cystidia. In *Mycena lasiosperma* Bres.,⁸ the ends of the cystidia are several times branched. The ends of the cystidia in several species of *Pluteus*⁹ are branched into a group of verticillate prongs. Their presence, absence, or variability in certain genera is as often accounted for by the action of the systematist as by any natural relationship of the forms.—GEO. F. ATKINSON.

Salt marsh development.—The theories advanced for the origin and development of salt marshes, with their typical plant associations, have postulated a shore being built up in bays, estuaries, and barrier-protected lagoons by organic matter resulting from the marsh vegetation and its entangled silt, resulting in a progressive plant succession. Recently DAVIS¹⁰ studied numerous sections of salt marshes in the vicinity of Boston, and found that the deposits were largely composed of the remains of salt marsh plants growing only within a vertical range of about three feet from high tide; and still more remarkable, thick beds of peat formed almost entirely from turf built by *Spartina patens*, a salt marsh grass with even more restricted vertical range. In other instances fresh water deposits were found below the salt marsh peat. Similar but much more limited data previously presented by PENHALLOW, as a result of investigations on the Maine coast, in an article reviewed in this journal,¹¹ caused him to assign to the phenomena the same explanation as that now given by DAVIS, namely, that the coast has for centuries been gradually subsiding. Peat deposits sixteen feet in thickness indicate this as the minimum amount of subsidence in the Boston area. This region, therefore, would present an interesting example of a static plant formation as a response to an actively dynamic topography, the rate of upbuilding by the vegetation being the same as that of the coastal subsidence. That subsidence was not constantly maintained throughout the entire period of time required for the formation of the deposits under investigation is shown by the presence of at least one bed of fresh water peat including tree stumps between two layers of *Spartina patens* turf.

Further evidence of a similar character is furnished by BARTLETT¹² from a study of a marsh at Woods Hole (Mass.), where similar peat deposits were found with large stumps of *Chamaecyparis thyoides* upon the beach where they were submerged at high tide and yet under conditions where there could have been no lowering due to undermining. Sections of this marsh also showed fresh water deposits sixteen feet below the present high tide level. Such data

⁸ Fung. Trid. 1:33. pl. 37. fig. 1. 1883.

⁹ For example, see *Pluteus cervinus* in PATOUILLARD, N., Tab. Analyt. Fung. 1:152. pl. 335. 1885.

¹⁰ DAVIS, CHARLES A., Salt marsh formation near Boston and its geological significance. Economic Geology 5:623-639. 1910.

¹¹ BOT. GAZETTE 45:352. 1908.

¹² BARTLETT, HARLEY H., The submarine *Chamaecyparis* bog at Woods Hole, Mass. Rhodora 11:221-235. 1909.

necessitate a modification of the current theories for the development of salt marshes, and lead DAVIS to conclude that "salt marshes in the area under consideration are features of and an accompaniment to coastal subsidence." The rate of subsidence is variously estimated by these and other investigators at from rather less than one foot per century to double that amount.

BARTLETT shows that a close relation exists between the chlorine content of the soil water and the limits of the various plant associations in the salt marsh. Similar data are given by HARSHBERGER¹³ for some of the salt marshes of New Jersey. These are mostly formed behind barrier beaches and are of relatively small area. Probably the most valuable portions of this paper are careful plant lists and the plotting of the vegetation of various typical areas, which will permit further investigators to trace with exactness the development and succession of the various plant associations. It also affords records of the natural vegetation in a region where man is making such changes in the surface and drainage that the original plant associations are rapidly disappearing. Similar records are also given for certain fresh water ponds and swamps formed by the advance of sand dunes across the outlet of various streams.—GEO. D. FULLER.

Biological life forms.—RAUNKIAER's application of his biological life forms to phytogeography has been translated into German by Miss TOBLER,¹⁴ so that his interesting results are now available to a wider circle of readers. His classification of plants into thirty biological types, based primarily upon the method by which the plant passes the unfavorable season of the year, has already been discussed in this journal.¹⁵ These have now been reduced to ten somewhat broader groups: stem succulents, epiphytes, megaphanerophytes and mesophanerophytes, microphanerophytes, nanophanerophytes, chamaephytes, hemicryptophytes, geophytes, helophytes and hydrophytes, and therophytes or annuals. The flora of a region is then classified into these ten groups, and the number of species in each group expressed in per cent of the total. This numerical arrangement is called a biological spectrum. By arranging these spectra for different regions in order, there is given an easy method of comparing the life forms of vegetation, not only with each other, but also with the flora of the world as a whole. From these spectra it is seen that the tropics are characterized by an excess of the various classes of phanerophytes, deserts by chamaephytes and therophytes, the temperate zone by hemicryptophytes, and the arctics by hemicryptophytes and chamaephytes. For the more northern floras the author finds that the number of chamaephytes

¹³ HARSHBERGER, JOHN W., The vegetation of the salt marshes and of the salt and fresh water ponds of northern coastal New Jersey. Proc. Acad. Nat. Sci. Philadelphia 61:373-400. 1909.

¹⁴ RAUNKIAER, C., Statistik der Lebensformen als Grundlage für die biologische Pflanzengeographie. Beih. Bot. Centralbl. 27²:171-206. 1910.

¹⁵ BOT. GAZETTE 44:392. 1907.

is especially significant. From an exhaustive study of local floras he has drawn circumpolar biochores, connecting regions with similar proportions of chamaephytes. The biochores of 10 per cent, 20 per cent, and 30 per cent are chosen to separate four floral zones, which he distinguishes as follows: a cold temperate or hemicryptophyte zone, south of the 10 per cent biochore; a boreal zone, between the 10 per cent and 20 per cent biochores; an arctic zone, between the 20 per cent and 30 per cent biochores; and an arctic-nival zone beyond the 30 per cent line. The same methods are also applied to alpine floras, and the number of chamaephytes is found to increase in the same way with the altitude. RAUNKIAER's chief object is apparently the recognition of certain types of climate, the results of which are expressed in the vegetation. His methods will probably have a much greater value in characterizing floral regions, irrespective of their climate, and will have the great advantage of basing the distinctions between regions upon the plants themselves, rather than upon any physical feature of the environment. It remains to be seen whether his chief biochores, chosen at certain round numbers and from one life form only, will eventually prove to be the most important.—H. A. GLEASON.

Gas movement.—OHNO¹⁶ has uncovered a most interesting situation in the rapid gaseous output from the leaf of *Nelumbo nucifera*. It is borne some distance above the water, and in the central region over the petiole there is a considerable depression. If on a warm sunny day one places some water in this depression, he will see a rapid extrusion of gas, which amounts to several times the volume of the leaf in a relatively short period. Analysis shows that the gas contains the percentage of O₂ found in air. A like volume is given off by a detached leaf with its petiole in water, even in darkness if the upper surface is warmed. All these facts show that it is not O₂ produced by photosynthesis, and indicate that it is air. Any condition that keeps the air over the leaf dry, sets up such an extrusion of gas. The phenomenon is best explained by the behavior of a model made by OHNO, which he states is a modification of forms before used, to show, in other connections, the physical principle which he believes is applicable here.

A porous clay cup is filled with moist sphagnum and the open end supplied with a one-holed rubber stopper and glass and rubber tubing. The end of the latter dips just a little under the water. The porous cup is heated gently on a warming stage. The air begins streaming out of the tube and continues until it amounts to several times the volume of the porous cup. It ceases only when the water supply of the sphagnum is exhausted. The air on the outside of the tube is relatively dry and the gas pressure there is mainly air. Inside there is a considerable water vapor pressure which decreases the air density. For this reason there is an inward diffusion of air, and, according to the Graham law, an even more rapid outward diffusion of water vapor. The lost water vapor is constantly resupplied by the moist sphagnum. There results an

¹⁶ OHNO, N., Ueber lebhaftes Gasausscheidung aus den Blättern von *Nelumbo nucifera* Gaertn. Zeitschr. Bot. 2:641-664. 1910.

increased internal pressure of gas which causes the streaming from the tube. This continues until the sphagnum is dry.

OHNO conceived that the leaf of *Nelumbo* acts in a similar way, taking in the air thus by diffusion, which increases the internal pressure and leads to an extrusion at the central region where the texture is loose. He examined a number of other plants, but found no other case of a similar exchange.—
WILLIAM CROCKER.

Respiratory intensity.—ROSÉ¹⁷ finds that the respiratory intensities of leaves, measured by cc. of CO₂ given off per hour per gram of green weight, varies with the illumination under which the plant is grown, and also with the stage of development of the plant. *Pisum sativum* and *Teucrium Scorodonia* were grown under cloth screens of various thicknesses. The light stopped by the screens was measured by means of a Vidal photometer. ROSÉ used four light intensities: V is full sunlight, IV is $V-2x$, III is $V-16x$, II is $V-22x$, x being the amount of light absorbed by a 5 mm. glass plate. Leaves were taken from the plants at different stages of their development, inclosed in a chamber with a known quantity of air, and put in a dark room. After a time the gas in the chamber was analyzed. For *Pisum sativum*, when two leaves have developed, the maximum respiratory intensity was found to be at illumination V, and there is a gradual decrease to II; but in the later stages the maximum is either at III, with a secondary increase at V, or the reverse. ROSÉ found that the structure of leaves developed under III and II was greatly modified. There was less lignified tissue and less cellulose; therefore, he thinks, there must be a greater amount of protoplasm and of carbohydrates in a given weight of leaf. There is less water in III than in II, therefore a greater percentage of oxidizable substance per gram of green weight. So, the author says, the respiratory maximum is displaced from V, the place of greatest dry weight, to III, the place of greatest amount of oxidizable substances. *Teucrium Scorodonia*, on the other hand, being a shade plant, has its greatest respiratory energy at IV, with its greatest dry weight.

The author's explanations of his results are not convincing. Some quantitative determinations of the enzymes present would be of value. The results found for leaves under the different illuminations would have been more nearly comparable if the water variant had been eliminated by measuring the respiration for a unit of dry weight.—SOPHIA ECKERSON.

Sporogenous tissue of Piper Betel.—The work of JOHNSON among Piperaceae is well known to morphologists, and he has now extended it by including *P. Betel monoicum*,¹⁸ a climbing Jamaican species with monosporangiate

¹⁷ ROSÉ, EDMOND, Énergie respiratoire chez les plantes cultivées à divers éclaircissements. Rev. Gén. Botanique 22:385-398. 1910.

¹⁸ JOHNSON, DUNCAN S., Studies in the development of the Piperaceae. I. The suppression and extension of sporogenous tissue in the flower of *Piper Betel* L. var. *monoicum* C. DC. Jour. Exp. Zool. 9:715-749. figs. 71 (year of publication not cited in separate).

flowers and immersed ovaries. The form is interesting in being dioecious, monoecious, or "monoeciously polygamous." The development of the sporangiate structures is of the usual angiospermous type. It is noteworthy that 100 or more antipodals appear and persist in the seed, although they contain little reserve food, which occurs chiefly in the starchy perisperm.

Chief attention, however, is given to the extreme variability in the development of sporogenous tissue as shown by different spikes or by different flowers of the same spike. The number of microsporangia produced by a stamen may vary from none to four, and the extent of a sporangium is widely variable. The point is made that these differences are not determined during the course of development, but are constant from the time of the initiation of the sporogenous tissue. Space relations in the spike hold no relation to the differences, for any condition may develop at any region of the spike. All that the author can suggest is that "the real cause is probably to be sought in those factors, internal or external, that disturb the normal production or course of movement of material in the plant."

Incidentally, the author concludes "that the tissue of the young spike, and often of the individual flower, must be hermaphrodite in character," since the differentiation of the two kinds of sporogenous tissue, involving the subsequent development of the two kinds of sexual tissue, "must take place at or after the initiation of the rudiments of the parts of the flower."—J. M. C.

Philippine forests.—WHITFORD'S continued investigations in the Philippine forests are making us better acquainted with tropical vegetation in comparison with the more familiar vegetation of the United States and Europe. A recent paper gives a detailed account of the forests dominated by members of the Dipterocarpaceae, a family whose name has to most of us an unfamiliar sound, though in the Philippines it is even more important than are pines and oaks with us, since it makes up 75 per cent of the virgin forest area;¹⁹ of the 40,000 square miles of Philippine virgin forest, 30,000 square miles are dominated by dipterocarps. From the lumberman's point of view the dipterocarps may be divided into three categories: those which yield hard and durable timber; those which yield a timber comparable to that of our hard pines; and those whose timber qualities resemble those of our soft pines. Dipterocarp timber compares favorably as to commercial value with the more familiar timbers of Europe and the United States. While some forests of temperate regions surpass those of the Philippines in the matter of bulk, the latter perhaps equal any temperate forests when the amount of the annual increment is taken into account together with the bulk. The best forests are found where climatic, edaphic, and biotic factors are at their optimum. Obvious growth rings occur in some trees, but are lacking or obscure in others; as yet it is not

¹⁹ WHITFORD, H. N., Studies in the vegetation of the Philippines. I. The composition and volume of the dipterocarp forests of the Philippines. *Phil. Jour. Sci.* 4:699-725. pls. 7. 1909.

known whether the growth rings where found are annual or seasonal, but from the data now in hand it appears that the soft wood trees become mature in the Philippine tropical forest in one-half to two-thirds the time that is taken by similar trees in the climate of the northern United States.—H. C. COWLES.

A non-corticated Chara.—Material of such a form was studied by Miss SLUITER,²⁰ along with *C. contraria* and *C. dissoluta*. The non-corticated form appeared in a laboratory culture of *Nitella* which had died down, and was also found later during an excursion to the upper Zürich Sea in the region of Busskirch. The two problems the author set herself for solution are: (1) What are the relations between *Chara dissoluta* and *C. contraria*? (2) Does the constantly non-corticated form of Busskirch belong in the *C. contraria* group? Is it to be joined with *C. dissoluta*, or are the relations to other non-corticated forms closer?

The main work is divided into three parts: the development of the shoot and its side-organs in *C. contraria*; that in *C. dissoluta*; and that in the *Chara* from Busskirch. Each part is subdivided into the internal and external features. In the results and conclusions the author states that there is great agreement between *C. contraria* and *C. dissoluta* f. *helvetica*. She believes there is not sufficient evidence to consider the latter as one of the many forms of the former, and would not, from her investigation, place it next to *C. contraria*. As to the non-corticated *Chara* of Busskirch, the non-corticated forms of *C. coronata* and *C. stelligera*, which have appeared before in Europe, show no relation to it. Other non-corticated species are no more similar. The author decides that the form must fall in with *C. dissoluta* f. *helvetica* and *C. contraria*. She believes that it must be designated as *C. dissoluta* f. *helvetica*, and that the entirely non-corticated form can appear independently from a one-layered corticated form.—NORMA E. PFEIFFER.

Synapsis.—In a short but important paper, LAWSON²¹ presents an interpretation of synapsis entirely at variance with current views, and supports his interpretation with such convincing evidence that some of our current notions must be revised. The name synapsis implies that it is a contraction stage, and as such it has been regarded. LAWSON shows conclusively that there is no contraction of the chromatin mass during the phase known as synapsis. For illustration he has taken the pollen mother cells of *Smilacina*, because it is easy to get complete series of stages in a single section, but he has confirmed the results secured in this genus by a study of algae, fungi, bryophytes, pteridophytes, gymnosperms, and other angiosperms.

During the growth of the spore mother cell, the great accumulation of nuclear sap causes the nuclear cavity to expand until it reaches two or three

²⁰ SLUITER, CATHA. P., Beiträge zur Kenntnis von *Chara contraria* A. Braun und *Chara dissoluta* A. Braun. Bot. Zeit. 68: 125-168. pls. 4-8. figs. 21. 1910.

²¹ LAWSON, A. ANSTRUTHER, The phase of the nucleus known as synapsis. Trans. Roy. Soc. Edinburgh 47: 591-604. pls. 1, 2. 1911.

times its original size, the chromatin remaining in one place, while the rest of the nuclear cavity is occupied only by the sap. A complete series of measurements shows that the chromatin area has not diminished. Although there is no contraction, important changes take place in the chromatin during synapsis. There is some evidence that the reticulum of the resting nucleus is composed of a number of threads, and that this number corresponds to the diploid number of chromosomes. Further, the threads are double and there is no evidence of any blending or fusion, the actual reduction occurring much later than the period known as synapsis. A paper dealing with the details of reduction is to follow.—CHARLES J. CHAMBERLAIN.

Turgescence and respiration.—MAIGE and NICOLAS²² have performed some very interesting experiments upon the effect of turgescence upon respiration. The materials used were various buds, leaves, and embryos. The gas determinations were made by the Bonnier-Mangin method. The work is reported under three heads: effect of increase of turgescence, effect of decrease of turgescence, and effect of a decrease followed by an increase. A rise in turgescence is always followed by increased production of CO_2 , intake of O_2 , and an increase in the ratio CO_2/O_2 . A fall in turgescence produces similar but less marked effects in material taken directly from the plant or soaked for a period in 5 per cent sucrose. In material previously soaked in 10 or 20 per cent glucose, this treatment always gives a decrease in CO_2 , O_2 , and frequently in the CO_2/O_2 . Each change, in the decrease followed by the increase, generally gave an increase in CO_2 , O_2 , and CO_2/O_2 . These facts are new and most interesting, but the interpretations will not find universal acceptance. The authors believe that increased turgescence increases respiration by increasing growth; and decreased turgescence by concentrating the oxidizable solutes of the cell. The first stimulative effect they consider the greater. The authors postulate an optimum concentration for the oxidizable solutes of the cell, and attribute the reversal of behavior after treatment with the strong glucose solutions to this optimum being passed.—WILLIAM CROCKER.

New mesozoic plants.—JEFFREY²³ has described a new araucarian genus (*Woodworthia arizonica*) from a triassic forest of Arizona. The wood is of the *Araucarioxylon* type, but the short shoots are abietineous, and persisted in the wood of the trunk throughout the life of the tree. It is suggested that short shoots characterized the older coniferous stock, and that this would fit into the current explanation of the coniferous ovuliferous scale as a modified short shoot. The leaf traces did not persist in the secondary wood, as they do among the living araucarians, but JEFFREY does not regard persistent leaf traces as an ancestral character of the coniferous stock, as SEWARD and LIGNIER have claimed, but as a more recently acquired character. The testimony of *Wood-*

²² MAIGE, A., et NICOLAS, G., Recherches sur l'influence des variations de la turgescence sur la respiration de la cellule. Rev. Gén. Botanique 22:409-422. 1910.

²³ JEFFREY, E. C., A new araucarian genus from the Triassic. Proc. Boston Soc. Nat. Hist. 34:325-332. pls. 31, 32. 1910.

worthia is thought to strengthen the evidence of the approximation of Araucarineae and Abietineae in the early Mesozoic, and of the more primitive character of the latter.

The same investigator²⁴ has also published a new species of *Prepinus* from the Cretaceous of Martha's Vineyard, which differs from the type species of Staten Island in that the wood of the short shoots has numerous resin canals in two or more rows, and the pith is without sclerotic nests. The conclusion is reached that "ligneous resin canals" are features of the oldest Abietineae, as shown now by the structure of the archaic genus *Prepinus* and also by that of the oldest species of *Pityoxylon*.—J. M. C.

Chlorophyll and photosynthesis.—IRVING,²⁵ working in BLACKMAN'S laboratory, has studied the relation between the early development of chlorophyll and of the photosynthetic power. He finds that seedlings developing in darkness and later transferred to light, or developing from the first in light, are able to fix all CO₂ produced by respiration only after becoming almost fully green. When considerable photosynthetic power does appear, it develops rapidly. The author believes the photosynthetic activity up to this stage never fixes more than 10 per cent of the CO₂ produced by respiration, and never amounts to over 1 per cent of the activity after the full development of the chlorophyll. The following quotation from the summary shows the significance of the work: "We are forced to conclude that the first development of this function is not in any relation to the amount of chlorophyll produced, and that the amount of chlorophyll present is never a limiting factor to assimilation in these early stages of the assimilating organs. If this is so, then it must be some other component part of the photosynthetic machinery which controls the beginning of complete functional activity. This part is not developed by illumination so quickly as the green pigment is developed, and therefore the pigment, and other parts of the total machinery, lie idle at the stage we have examined, awaiting the developing of the last factor."—WILLIAM CROCKER.

Reduction divisions of *Oenothera*.—DAVIS²⁶ has published another confirmation of the earlier work of GATES²⁷ and of GEERTS²⁸ on reduction in

²⁴ JEFFREY, E. C., A new *Prepinus* from Martha's Vineyard. Proc. Boston Soc. Nat. Hist. 34:333-338. pls. 33. 1910.

²⁵ IRVING, A. A., The beginning of photosynthesis and the development of chlorophyll. Annals of Botany 24:805-818. 1910.

²⁶ DAVIS, B. M., The reduction divisions of *Oenothera biennis*. Annals of Botany 24:631-651. pls. 52, 53. 1910.

²⁷ GATES, R. R., Pollen development in hybrids of *Oenothera lutea* × *O. Lamarckiana*, and its relation to mutation. BOT. GAZETTE 43:81-115. pls. 2-4. 1907.

———, A study of reduction in *Oenothera rubrinervis*. BOT. GAZETTE 46:1-34. pls. 1-3. 1908.

———, The behavior of the chromosomes in *Oenothera lutea* × *O. gigas*. BOT. GAZETTE 48:179-199. pls. 12-14. 1909.

²⁸ GEERTS, J. M., Beiträge zur Kenntnis der Cytologie und der partiellen Sterilität von *Oenothera Lamarckiana*. Recueil Trav. Bot. Néerl. 5:93-208. 1909.

Oenothera. He gives the telosynaptic account, involving the segmentation of the thick spirem (pachynema) into a single chain of chromosomes. No new facts regarding reduction are brought out, and there are no deviations from the history of reduction as already known for *O. Lamarckiana* and its mutants. The reviewer, in a paper before the Botanical Society of America in 1908,²⁹ showed that the process of reduction in the mutating forms can be duplicated by figures of every stage in *O. biennis* and *O. laevifolia*, there being the same tendency not to form close pairs, and the same loose arrangement of the chromosomes on the heterotypic spindle. This permits of occasional irregularities in the distribution of the chromosomes during reduction, and these were found to occur in normal material of *O. biennis*, as in the mutating forms. Thus no differences in the method of reduction in the different species and races of *Oenothera* have yet been found, except in *O. grandiflora*, in which DAVIS³⁰ obtains what he thinks are rings, in the place of loose heterotypic bivalents. As the reviewer has already pointed out,³¹ the supposed rings are probably due to a greater attraction between homologous chromosomes in *O. grandiflora* than in the other forms.—R. R. GATES.

Florida peat deposits.—This report³² is the result of a general survey of peat formations and distribution in Florida, without detailed examination or studies. Immature topography affords the most favorable surface water conditions for deposit of peat if associated with proper climate, not too dry nor too cold, as in glaciated areas of eastern North America and of Europe, and in the Coastal Plain of the southeastern United States. Florida seems to offer ideal conditions, having a greater variety of swamps, bogs, marshes, and places where peat accumulates than any equal area in North America, and also an ample rainfall. A tentative classification of the peat is based on the nature of the water with which it was found associated: salty, muddy, calcareous, swamp waters, with several exceptional deposits. The best and deepest peat is that in the peat prairies classed as "filled lakes"; under the same division is included the northern everglades. Analyses of 53 samples indicate a good average quality, the fuel value being above the average for pressed peat (8500 B.T.U.; DAVIS) for two-thirds of the samples. The list of peat plants includes 83 families of angiosperms, 6 conifers, *Isoetes*, 2 lycopodiums, *Azolla* sp., 11 ferns, several mosses, and *Chara*.—LAURA GANO.

Sporangia of Weichselia.—This is a cretaceous genus of fernlike plants known heretofore only from the bipinnate sterile fronds. The question has

²⁹ GATES, R. R., Further studies of oenotheran cytology. *Science* N.S. **29**:269. 1909.

³⁰ DAVIS, B. M., Pollen development of *Oenothera grandiflora*. *Annals of Botany* **23**:551-571. pls. 41, 42. 1909.

³¹ BOT. GAZETTE **49**:64-66. 1910.

³² HARPER, ROLAND M., Preliminary report on the peat deposits of Florida. Included in third Ann. Rep. Fla. State Geol. Survey. 1910.

been raised whether it is not a belated member of the Cycadofilicales, and therefore any further information concerning it is desirable. BOMMER³³ has obtained material that supplies additional information, which he publishes in a preliminary announcement. The vascular structure of the plant suggests to him possible relationship with the Matoniaceae, but the sporangia, now found attached, are of special interest. They occur in synangia which resemble inverted cones, and possess an incomplete annulus, as in *Matonia*. Each synangium includes 10-15 sporangia, and the synangia themselves are grouped so as to form spherical bodies 3-4 mm. in diameter. These synangial groups are borne thickly on apparently naked branches of the frond. Such fructifications have been found heretofore detached. BOMMER is evidently undecided whether the most obvious testimony at present should decide for *Matonia* affinities; or whether certain vague suggestions should decide for a *Marattia* connection; or whether, after all, these synangia may not be the microsporangia of Cycadofilicales. This lack of decision is commendable.—J. M. C.

A classification of plants.—Professor BESSEY has long been interested in a general classification of plants which is quite a departure, in many respects, from current schemes. In 1909 he published in outline his ripened conclusions, together with the principles involved, and now he has furnished a key³⁴ by which the groupings are defined, so far as a key can define. It is impossible to give an account of the views expressed without reprinting the paper, for it is in itself the shortest possible statement. It is sufficient to say that the 4 conventional main groups are dissipated into 14 "phyla," whose technical and common names may serve to indicate them: Myxophyceae (slime algae), Protophyceae (simple algae), Zygomyceteae (conjugate algae), Siphonophyceae (tube algae), Phaeophyceae (brown algae), Carpophyceae (higher algae), Carpomyceteae (higher fungi), Bryophyta (mosses), Pteridophyta (ferns), Calamophyta (calamites), Lepidophyta (lycopods), Cycadophyta (cycads), Strobilophyta (conifers), Anthophyta (flowering plants). These phyla are broken up into 32 classes and 94 orders, not including the dicotyledons, which constitute class 33, with 5 "super-orders," the list of orders not being given.—J. M. C.

Seeds of the Conostoma group.—OLIVER and SALISBURY³⁵ have assembled the material of *Conostoma* for investigation, and have compared it with *Lagenostoma*, *Physostoma*, and *Gnetopsis*. A full description is given of *C. oblongum* and *C. anglo-germanicum*, and this is followed by a comparison with related

³³ BOMMER, CH., Contribution à l'étude du genre *Weichselia*. Note préliminaire. Bull. Soc. Roy. Bot. Belgique 47:296-304. figs. 18. 1911.

³⁴ BESSEY, CHARLES E., The phyla, classes, and orders of plants. Trans. Amer. Micr. Soc. 29:85-96. 1910.

³⁵ OLIVER, F. W., and SALISBURY, E. J., On the structure and affinities of the paleozoic seeds of the *Conostoma* group. Annals of Botany 25:1-50. pls. 1-3. figs. 13. 1911.

types and a taxonomic presentation of the group, in which *Gnetopsis elliptica* is placed provisionally with *Conostomum* in the "Conostomeae." A brief discussion of the "pollination mechanisms" of the Lagenostomales calls attention to the three distinct types exhibited by the group: that in which the free but approximated lobes of the integument surrounded and overtopped the pollen chamber and probably at pollination formed a funnel (*Phylostoma*); that in which a massive "canopy" was pierced by a long micropyle (*Conostoma*); and that in which the compact canopy closely invested the conical pollen chamber, whose orifice reached to the outer surface (*Lagenostoma*). A glossary is provided at the close of the paper, since such terms as the "blow-off layer," "lagenostome," and "plinth" are not easily separated from the well-worn terms heretofore applied to the same structures.—J. M. C.

Anatomy of Azolla.—QUEVA³⁶ has investigated the vascular anatomy of *Azolla filiculoides*, and has secured some interesting facts. The vascular elements are differentiated in the floating, dorsiventral stem, those of the dorsal region being tracheids of small caliber, and those of the ventral region being vessels of large caliber. The transverse section of the xylem is circular, the circle being incomplete alternately on the right and left sides in the dorsal region; so that the section is really an arc which is open alternately right and left, corresponding to the alternating leaf traces. The heavy vessels of the ventral region are connected exclusively with the roots. The interpretation suggested is that the dorsal group of vessels represents a reduced bipolar group, connected at the poles with leaf traces; and that the ventral group is merely an "apolar" mass related to the roots. The amount of vascular tissue retained would seem to be a remarkable feature in a stem with such an extremely hydrophytic habit.—J. M. C.

Germination of Helianthus.—MILLER³⁷ has studied the transformations of the reserve materials of the sunflower during germination. The work shows both chemical and biological excellence. Main emphasis is put upon the transformation of fats. The fats extracted from the cotyledons show low acid values at all times, while those from the hypocotyl very early, and continuously thereafter, show high acid values. It was not determined whether the fats are translocated as such or as hydrolyzed products. The iodine value of the fats falls as germination advances, due as the author believes to the absorption of oxygen. As germination progresses, the fats decrease rather rapidly, while the carbohydrates increase. This furnishes further evidence for the established view that during germination fats are transformed to carbohydrates.—WILLIAM CROCKER.

³⁶ QUEVA, C., L'*Azolla filiculoides* Lam., étude anatomique. Mém. Soc. Hist. Nat. Autun 23: pp. 24. figs. 22. 1910.

³⁷ MILLER, EDWIN C., A physiological study of the germination of *Helianthus annuus*. Annals of Botany 24: 693-726. 1910.

Geotropism of hypocotyls and cotyledons.—SCHÜTZE,³⁸ working in PFEFFER's laboratory, has published a paper on the geotropic behavior of hypocotyls and cotyledons. The work adds some facts to that of COPELAND³⁹ on this subject. For hypocotyls, *Phaseolus multiflorus*, *P. vulgaris*, *Helianthus annuus*, *Cucurbita Pepo*, *Ricinus communis*, *Vicia Faba*, and others were used; and for cotyledons, *Phoenix dactylifera* and *Yucca angustifolia*. Both the cotyledons and hypocotyls showed positive geotropic reaction after the removal of the root tips. Traumatropic response followed a one-sided injury of the root tip. The change from positive to negative geotropism always begins at the base of the hypocotyl and travels upward. The zone of most rapid growth always accompanies this zone of change.—WILLIAM CROCKER.

Ovule of Bruniaceae.—This is a family of 12 genera, endemic in South Africa, and one of the group of families that forms a penumbra about the Saxifragaceae. So isolated does it seem, that SAXTON⁴⁰ has investigated the structure of the ovule and embryo sac. He finds a single massive integument, and in *Brunia* an embryo sac completely replacing the nucellus and packed with starch, which almost completely disappears before fertilization; in *Berzelia* and *Staavia* a little of the basal nucellar tissue persists. The solitary megaspore mother cell and the tetrad present nothing unusual; and, so far as the ovular structures are concerned, there is nothing suggestive of relationship. Certainly there is no suggestion of an "ancient type," especially since a single massive integument is a feature of the Sympetalae.—J. M. C.

Evaporation in Jamaica.—Observations made by BROWN⁴¹ on the grounds of the Cinchona Laboratory of the New York Botanical Garden in the Blue Mountains of Jamaica, extending over a period of 25 days in May and June 1910, give an unexpectedly low rate of evaporation even in an open grassy clearing (8.2 cc. daily); while in a densely wooded ravine it was less than 1 cc. daily from the standard Livingston atmometer. The use of the non-rain-absorbing atmometer is here reported for the first time, and its results show that, while the general relation of two or more evaporation rates remains the same as for the ordinary atmometer, the numerical factor differs and must approach more nearly to an absolute determination when the non-rain-absorbing instrument is used.—GEO. D. FULLER.

Mistletoe.—YORK⁴² has made an anatomical and ecological study of the American mistletoe, confirming several well known facts, such as its dissemi-

³⁸ SCHÜTZE, RUD., Ueber das geotropische Verhalten des Hypokotyls und des Kotyledons. Jahrb. Wiss. Bot. 48:377-423. 1910.

³⁹ BOT. GAZETTE 31:410-422. 1901.

⁴⁰ SAXTON, W. T., The ovule of the Bruniaceae. Trans. Roy. Soc. S. Africa 21:27-31. figs. 8. 1910.

⁴¹ BROWN, WM. H., Evaporation and plant habitats in Jamaica. Plant World 13:268-272. 1910.

⁴² YORK, H. H., The anatomy and some of the biological aspects of the "American mistletoe," *Phoradendron flavescens* (Pursh) Nutt. Bull. Univ. Texas 120. pls. 13. 1909.

nation by birds, its water parasitism, its essentially xerophytic structure, and the distortion which it causes in the branches of its host plants. The chief hosts in the vicinity of Austin, Texas, are the hackberry, elm, mesquite, and osage orange. The immunity of certain trees (as the China tree and box elder) appears to be due to the character of the external surface and the thickness of the corky layer.—H. C. COWLES.

Statolith theory.—NĚMEC⁴³ controverts PEKELHARING's claim that roots respond to the geotropic stimulus after being freed from statolith starch by growing in 0.025 per cent potassium alum. Aside from potassium alum, NĚMEC used aluminum sulphate and chloride and zinc sulphate as destarching agents. In no case was geotropic response given in absence of statolith starch. With such treatments, marked injury always accompanied absence of starch. He believes that the statolith theory stands in the face of all suggested evidence against it.—WILLIAM CROCKER.

Cytology of Spongospora.⁴⁴—In the current issue of the *Annals of Botany* two investigators present preliminary accounts of their investigations on *Spongospora*, the organism which causes the powdery or corky scab of the potato. Both describe the life history, both note that chromatin at certain stages takes the form of chromidia, and both note resemblances to *Plasmodiophora*, OSBORN suggesting that *Spongospora* should be placed in the Plasmodiophoraceae.—CHARLES J. CHAMBERLAIN.

Light perception.—HABERLANDT⁴⁵ answers Wager's arguments against the lens theory of light perception by foliage leaves. In places his answer shows keen retort, though it often lacks any convincing evidence. Such are the methods to which one must resort when one defends a questionable though favorite hypothesis.—WILLIAM CROCKER.

⁴³ NĚMEC, B., Der Geotropismus entstärkter Wurzeln. Ber. Deutsch. Bot. Gesell. 28:107-112. 1910.

⁴⁴ OSBORN, T. G. B., A preliminary note on the life history and cytology of *Spongospora subterranea* Wallroth. Annals of Botany 25:271. 1911.

HORNE, A. S., Preliminary note on *Spongospora solani* Brunch. Annals of Botany 25:272. 1911.

⁴⁵ HABERLANDT, G., H. WAGER's Einwände gegen meine Theorie der Lichtperzeption in den Laubblätter. Jahrb. Wiss. Bot. 48:337-390. 1910.

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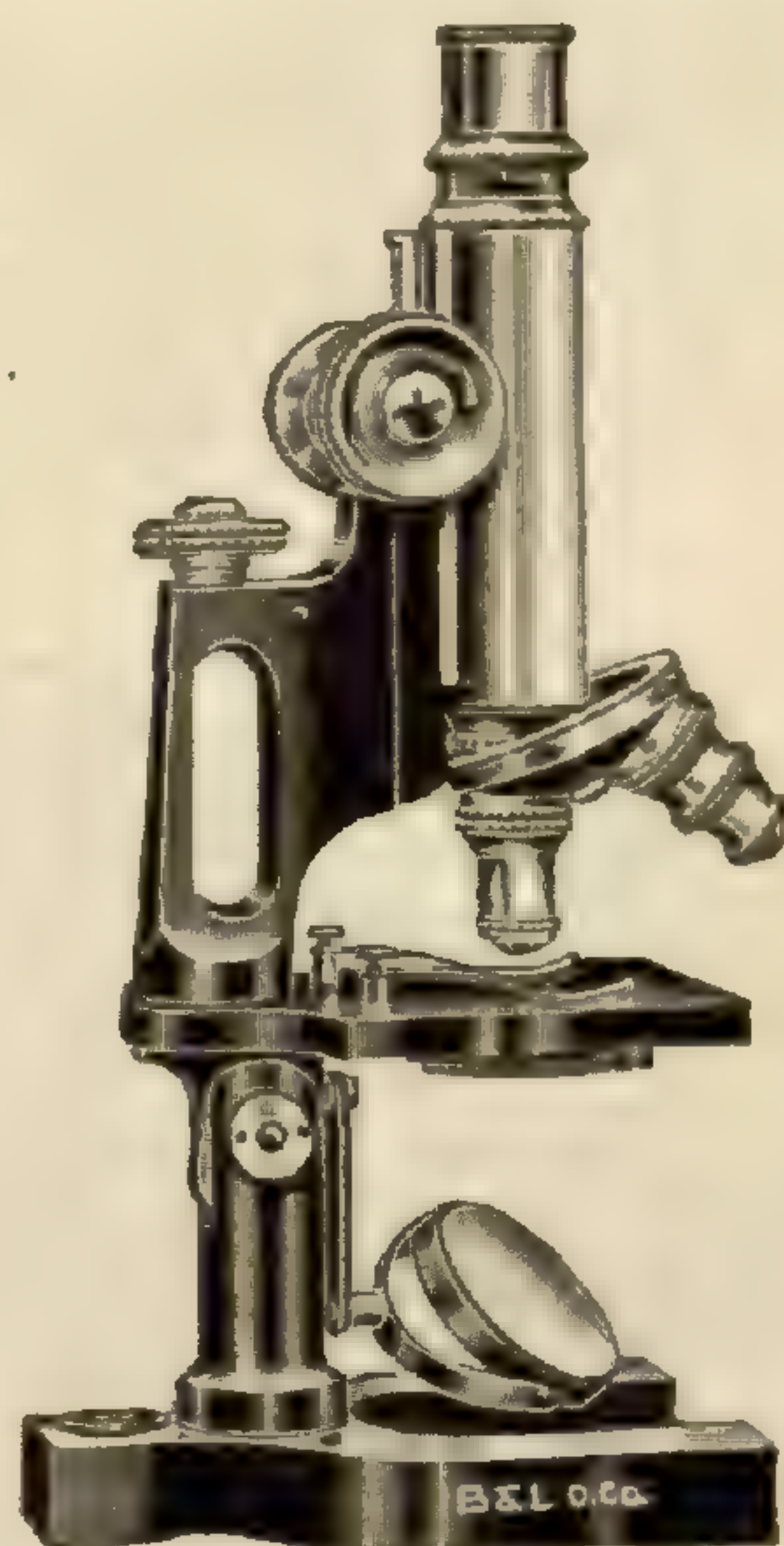
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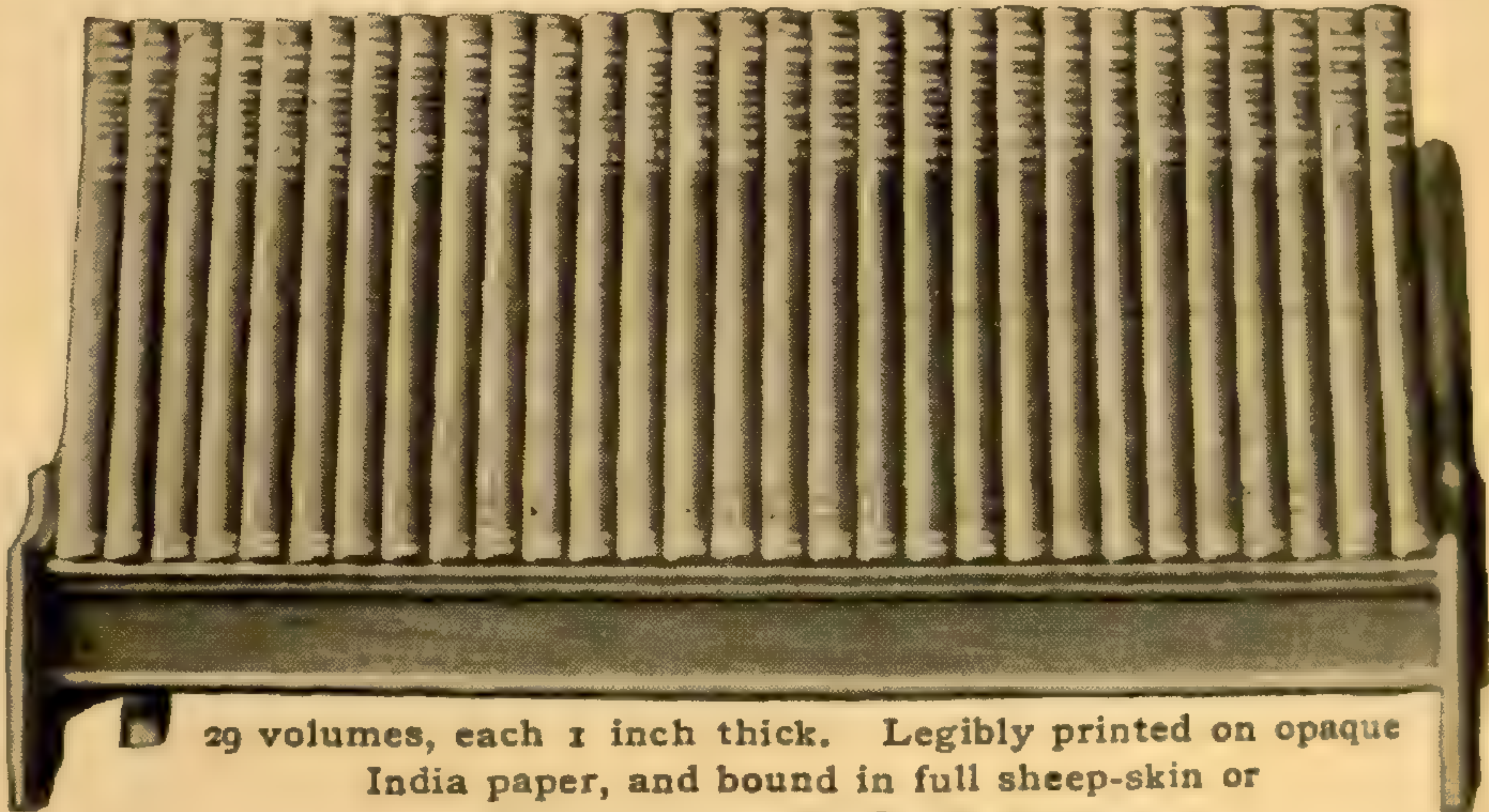
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THE BOTANICAL GAZETTE

MAY 1911

THE MODE OF CHROMOSOME REDUCTION¹

REGINALD RUGGLES GATES

In 1894 STRASBURGER (22), in his well-known paper in the *Annals of Botany*, placed the alternation of generations in plants on a chromosome basis, and showed that not only does a reduction of the chromosomes take place which marks the passage from sporophyte to gametophyte, but that the reduced or gametophytic number is phylogenetically the primitive number, the dominance of the sporophyte with the diploid number in the life cycle having been reached chiefly in the higher phyla of plants.

The stimulus to investigation resulting in part from that paper has led to two results: (1) the determination, for many members of each plant group, of the point in the life cycle where reduction occurs; and (2) the detailed investigation of the exact method by which the process of chromosome reduction is effected. The former line of activity has led to a clear understanding of the life cycle in nearly all plants, and is therefore of fundamental significance for plant morphology. The latter line of inquiry has led to the expression, during the last fifteen years, of a great variety of opinions concerning the precise nature of the reduction process, such opinions affecting fundamentally our conceptions regarding the nature of the chromosomes themselves and the part they play in hereditary processes. These cytological investigations, having gone forward simultaneously on plants and animals, have served to prove the fundamental unity and universality of meiotic phenomena in sexual organisms, so that the present-day cytologist

¹ The main features of this paper were presented by invitation before the National Academy of Sciences, St. Louis Meeting, November 8, 1910.

must take cognizance of the extensive literature on this subject concerning both plants and animals, and also the rapidly developing field of experimental cytology, in making his interpretations and drawing his conclusions. Nowhere is the fundamental unity of all organic matter better exemplified than in the study of these nuclear processes.

It is not my purpose to trace the history of the many changes of opinion regarding the method of chromosome reduction which have occurred as our knowledge of this process has developed. I wish merely to consider certain of the current views, and to express my own point of view, which has resulted from careful studies of reduction in various races and species of *Oenothera*, and the comparison with many other forms,² both from preparations and from the literature, as well as from a consideration of the many important data from experimental cytology, and the crossing of forms whose chromosomes differ in number or in morphology. This point of view, therefore, results from the consideration of data bearing on the chromosome question from every angle, so that it would be useless to attempt a citation of all the facts upon which it is based. Nor shall I attempt in this paper to formulate a complete hypothesis of chromosome behavior, nor of the precise hereditary rôle of the chromosomes. My special endeavor will be to show how the chief divergent current opinions regarding meiosis may be unified and harmonized. This will of course involve incidentally the expression of certain views regarding the nature of the chromosomes themselves. I regard it as the duty of every discoverer of new facts to bring them into relation, and if possible into harmony, with the other authenticated facts in the same field. The present paper is an attempt to fulfil this function with regard to my own studies on chromosome reduction. To do this in the present state of our knowledge of this process requires that the subject be approached from a broader viewpoint, if the

² I am greatly indebted to Professor GRÉGOIRE for kindly giving me the use of his laboratory facilities during my stay at Louvain, and for many animated and critical discussions of current cytological problems. I am also indebted to Professor STRASBURGER for the courtesies of his laboratory, and for the privilege of examining a large number of cytological preparations. I alone, however, am responsible for the views here expressed.

different methods described are to be welded into one. Perhaps it may also be hoped that the viewpoint here developed will help to stimulate some of the further investigations on this fascinating subject.

Much of the confusion and change of opinion with regard to meiotic phenomena have come from the study of different stages of the process at different times. The earlier investigators of this subject devoted their attention almost entirely to the study of the heterotypic chromosomes or "tetrads," and the manner of distribution of the elements of which each was composed. It was chiefly in later studies that the necessity for determining the manner of origin of the heterotypic chromosomes was realized, so that the studies of the last five or six years have been directed mainly to an understanding of the earlier stages of meiosis, from the telophase of the last premeiotic mitosis to diakinesis. These include the leptonema, zygonema, pachynema, and strepsinema stages (names, some of which involve different interpretations), all of which GRÉGOIRE (12, p. 239) prefers to include under the general term synapsis. The synizesis, a special name proposed by McCLUNG (13) for the stage when the delicate chromatic threads occupy but a small part of the nuclear cavity, is also included in this period. In this paper I shall use the term synapsis in its more restricted and more usual botanical sense, as equivalent to synizesis.

The later stages of meiosis, from diakinesis onward, are now pretty clearly understood and agreed upon by most cytologists, particularly those who have studied plant forms. It is the events of the earlier stages which are still in dispute. Some of the most useful contributions of the most recent papers have been with regard to the earliest stages of all, from the "resting" reticulum of the spore mother cell to the synizesis condition.

The use of the term "tetrads" as applied to the heterotypic chromosomes by nearly all the earlier students of meiosis, both in plants and animals, has led to much confusion, due to the fact that these bodies exhibit a great variety of forms and appearances, and in many cases are not tetravalent at all, but bivalent or gemini, and are not due to the split of a single body, but to the approxi-

mation of two somatic chromosomes which may or may not show fission. The attempt to interpret bivalent structures as "tetrads" has been a frequent source of error. The significance of the term "tetrad" as applying to the heterotypic chromosomes was of course derived from the supposed theoretical implications, derived from WEISMANN'S distinction between a longitudinal or quantitative, and a transverse or qualitative division of the chromosomes. It was assumed that if the heterotypic chromosomes gave the appearance of being tetrads or tetravalent structures, then they must have originated from two segmentations, one of which was longitudinal of the spirem and the other transverse. This conception has since lost much of its usefulness, and this is a case where the too close adherence to a useful and stimulating theory has tended finally to retard progress. While such a difference is not impossible, it has not yet been shown by critical observation or experiment that there is any fundamental distinction between a longitudinal and a transverse segmentation of a chromosome. But, on the other hand, many facts with regard to chromosome continuity or individuality of a certain type must be regarded as well established. Longitudinal fission of all the chromosomes is regarded as universal in somatic mitoses, and this has frequently been pointed to as a strong argument in favor of the view that a chromosome is composed of qualitatively different portions or bodies arranged along its long diameter, whose equal division and distribution it is the function of this longitudinal fission to bring about. But it may be pointed out that this longitudinal fission of the viscous chromosome bodies may be determined by purely physical forces resulting, for example, from the electrical charges carried by the chromatin particles.

If this were the case, instead of an equal distribution of "ids" to each daughter chromosome, longitudinal fission would mean merely fission for mechanical or physical reasons along whatever becomes the longitudinal axis of the chromosome as it changes from the reticulate condition of the resting nucleus to the compact condition of prophase or metaphase. There is no observational evidence that longitudinal fission means any more than this, nor that in the passage from the alveolate or reticulate condition of the

resting nucleus to the compact condition of the prophase, any particular arrangement of differential units of structure composing an individual chromosome takes place.

Studies of forms whose chromosome group is composed of bodies morphologically unlike (heteromorphic) have shown, for example in various insects, that the chromosomes frequently maintain the same space relationships to each other in each equatorial plate, and therefore also probably during the intervening "resting" conditions of the nuclei. Other clear evidence, given, for example, by BOVERI (I and Ia), leads to the same conclusion. Hence it is probable that the direction of the long axis of the chromosomes, and hence their plane of division, correspond in successive mitoses. It does not therefore follow, from the statements of the last paragraph, that there is no difference between a longitudinal and a transverse division of a somatic chromosome. For even though such a transverse fission may be of no hereditary significance in separating unlike parts of a chromosome, yet it may have an important mechanical significance, and as far as the morphology of the product is concerned, the result of a transverse split of certain chromosomes in a nuclear plate may very well be different from that of a longitudinal fission. STRASBURGER (25, p. 437) suggests as an explanation of the heteromorphic chromosomes in such forms as *Funkia*, *Yucca*, and *Galtonia* that the short chromosomes have arisen by the transverse segmentation of certain of the long chromosomes. This may have been a consequence of the differentiation of the parts of such chromosomes, or may have resulted from more purely mechanical causes, but at any rate it furnishes no evidence that successive longitudinal segments of the long chromosomes which maintain their unity are unlike.³ Therefore, although, phylogenetically considered, transverse segmentations of members of the chromosome group have doubtless occurred in various species, it does not follow that these segmentations have any fundamental hereditary significance,

³ In a few forms, such as *Ascaris*, having very few chromosomes, they appear to be compound structures, as shown by their fragmentation in somatic mitoses; but in the great majority of forms no evidence of the compound character of the chromosomes is forthcoming.

because the products of the segmentation all remain in the same nucleus and are propagated in each mitosis.

There is, therefore, no satisfactory cytological evidence that the chromosomes are composed of smaller units whose equal division and distribution is brought about in each mitosis. According to the most careful cytological studies, we cannot with any assurance affirm the existence of smaller differential units composing the chromosomes. On the other hand, the many lines of evidence indicating the more or less independent behavior and genetic continuity of the chromosomes within a nucleus from mitosis to mitosis in the vast majority of cases, seems clear and incontrovertible. To the writer, this independence of behavior will find an explanation in some difference, probably of a chemical nature, between the materials of which the individual chromosomes are composed.

That this is insufficient, however, as an entire explanation, seems to be shown by the case of *Oenothera gigas* (GATES 6). This mutant has 28 chromosomes, double the number found in its parent, *O. Lamarckiana*. As stated in the above-mentioned paper, *O. gigas* probably contains merely a duplicate set of *O. Lamarckiana* chromosomes, although other changes seem to have occurred simultaneously in producing the mutation. The new number of chromosomes persists, however, and this shows that even though certain of the chromosomes are as much alike as two chloroplasts, yet, having occurred in a given nucleus, they will reappear in its descendants. This may be accounted for by the fact that the mitotic mechanism brings about a simultaneous division of all the chromosomes present. But it does not account for the further fact that all these bodies reappear in the prophase of each mitosis, and hence must have maintained their identity in some way while in the alveolated and distributed condition of the resting nucleus.

The lines of evidence which favor this conception of chromosome continuity from mitosis to mitosis are too numerous to enumerate, and since this view in some form is now widely accepted by cytologists, an enumeration is unnecessary in the present connection. One clear result showing the unity in behavior of the chromosomes was found in the hybrid *O. lata* × *O. gigas* (5). This hybrid had 21 chromosomes, 7 derived from the *O. lata* egg and

14 from the *O. gigas* male cell. In reduction they segregated regularly into groups of 10 and 11. The recent work on animal species and hybrids with heteromorphic chromosomes, by BOVERI, BALTZER, HERBST, TENNANT, and others, including the remarkable cases in which certain chromosomes are extruded, is all a confirmation of the same point of view.

We have thus reached the view that, while the chromosomes clearly behave as more or less independent units of structure, we are not justified by observational evidence in assuming that they in turn are composed of smaller morphological units. Further, what has frequently been interpreted as a transverse segmentation of the spirem or of the meiotic chromosome gemini is now known to be, in most cases at least, only the separation of whole somatic chromosomes. It may therefore be questioned whether a transverse fission of the chromosomes themselves ever regularly occurs. As already pointed out, however, this may be for purely mechanical or physical reasons.

From this point of view let us now examine the question of the method of chromosome reduction. In former papers (4, 5, 7) I have shown that reduction in *Oenothera* takes place according to the FARMER and MOORE method of telosynapsis, the spirem segmenting into a chain of chromosomes arranged end-to-end. In the heterotypic mitosis these (somatic) chromosomes, which may or may not be visibly in pairs, are segregated into two groups at the poles of the spindle. Each of these chromosomes undergoes a longitudinal split during the anaphase or telophase of the heterotypic mitosis, and the halves thus produced are distributed by the homotypic mitosis. The essential and critical stages which show that this is the method of reduction in *Oenothera* were presented in my paper of 1908. The suggestion of GRÉGOIRE, in his very useful summary of the literature of chromosome reduction (12, p. 325), that a strepsinema stage had been omitted between the pachynema and diakinesis, cannot apply. It is evident from an examination of figs. 18-32 in my paper already referred to (4) that such a stage cannot be intercalated. Especially figs. 18, 22, 23, and 24 leave no room for any other interpretation than the obvious one that a pachynema thread is segmenting into a chain

of chromosomes. Nothing but the exigencies of a theory would tempt anyone to suggest any other explanation. GEERTS (10), afterward confirmed by DAVIS (2), has reached the same conclusion.

I therefore regard it as certain that in *Oenothera* the pachynema segments directly into a chain of chromosomes arranged end-to-end. That one can reach such a degree of certainty on this point is largely due to the peculiarly favorable character of these critical stages in *Oenothera*, the chromosome number being small (14) and the chromosomes themselves being relatively short and stout, so that the difficulties attending the interpretation of the long threadlike chromosomes are not encountered here.

While, therefore, an end-to-end arrangement or telosynapsis of the chromosomes occurs in *Oenothera*, I think there is also adequate evidence of a side-by-side pairing, or parasynapsis, in certain other forms. I have presented this point of view in several papers (4, 5, 7), and have been further confirmed in it by my studies in other laboratories.

It is not necessary to specify here all the plants which are demonstrably telosynaptic, and those which are believed to be demonstrably parasynaptic, but a few of the cases which are best established may be cited. Among recent accounts, in addition to *Oenothera*, telosynapsis in plant forms seems to have been adequately shown by YAMANOUCHI (28) in *Fucus*. The most convincing recent accounts of parasynapsis have been by GRÉGOIRE (11) with figures of *Lilium*, *Osmunda*, and *Allium*; ROSENBERG (18) for *Drosera*; and YAMANOUCHI (27) for *Nephrodium*. In *Galtonia*, STRASBURGER first (23) gave a telosynaptic account. Later, MIYAKE (14) in STRASBURGER'S laboratory decided for parasynapsis. In certain of the later stages, *Galtonia* evidently resembles *Oenothera*. MIYAKE'S figures (pl. 3, figs. 23-32) indicate the segmentation of a pachynema into a chain of chromosomes. It was only after long search, as MIYAKE states (p. 96), that stages as represented by figs. 17-19 were found, indicating a lateral pairing of long narrow chromosomes (strepsinema). According to the ordinary method of cytological interpretation, he concludes that the latter stage must be intercalated, and that all the chromosomes always pass through the strepsinema stage of his fig. 18. This

interpretation assumes an unwarranted amount of "secondary fusion" between the chromosomes to form a chain, as indicated, for example, in his figs. 23 and 24. It seems to the writer equally justifiable to assume that the apparent rarity of a strepsinema stage is real, and that usually the chromosomes do not pass through such a stage during maturation. This obviates the necessity of finding an explanation for an amount of "secondary fusion" between the ends of the chromosomes, which is not easily accounted for. This has always been a serious stumbling-block for those who affirm the universality of parasynapsis, in which the pachynema is followed by a strepsinema stage.

Let us now inquire what is the exact difference involved between the methods of telosynapsis and parasynapsis as described in current papers. Telosynapsis involves the folding and looping and subsequent segmentation of a single thick thread (pachynema) which may have previously exhibited a split which closed up, to reappear only in the anaphase or telophase of the heterotypic mitosis as a longitudinal split in the components of the heterotypic gemini. Parasynapsis involves the lateral pairing of delicate threads at a stage earlier than the pachynema, their more or less complete fusion to form the pachynema, and their subsequent separation to form the strepsinema stage with paired threads, which, by shortening and thickening and (in the cases where a continuous pachynema or strepsinema spirem is supposed to be formed) transverse segmentation to form chromosome pairs, which when first formed are characteristically composed of two long and narrow threadlike chromosomes lying side-by-side and more or less coiled about each other. Later, by shortening and thickening, these chromosomes may, as in *Drosera* (ROSENBERG 18), become short and stout, or as in *Lilium* they may remain relatively long and narrow, even in diakinesis and the following metaphase.

I think it can be shown upon analysis that the difference between these two methods of reduction is far less fundamental than has been generally supposed.⁴ I further believe that the

⁴ A recent important paper by Miss DIGBY (2a) is quite in accord with this point of view. Miss DIGBY has made a fresh and careful study of somatic and meiotic divisions in *Galtonia*. She interprets the paired threads in early prophase of the

importance and significance of the synapsis stage, even though this condition is unique in the life cycle, has been greatly overestimated; and that the difference between the prophase of an ordinary somatic mitosis and that of the heterotypic mitosis (that is, the presynaptic and postsynaptic stages, from the resting reticulum of the last somatic mitosis to diakinesis) is much less fundamental in character than generally assumed in the current literature. The main fact of reduction, according to the most careful studies of either the telosynaptic or the parasynaptic method, is that in the heterotypic mitosis, instead of dividing, the chromosomes (which represent whole somatic chromosomes) segregate. Nor is there any adequate evidence that the mechanism of meiosis is meant to accomplish anything more than this. The reduction divisions have been studied without sufficient comparison with somatic mitoses, and it is probable that various features of the postsynaptic stages will be found to be devoid of any greater significance than attaches to corresponding spirem stages in the prophases of ordinary mitoses. Theories based on a supposed interchange of "chromomeres" or other materials during certain stages of the heterotypic prophase can be cast aside as having no cytological foundation in critical observation. The most careful recent studies have failed, not only to find any evidence for an interchange of chromomeres, but even to substantiate the idea that the chromatic threads are composed of linin in which chromatin granules are imbedded. The careful observations of GRÉGOIRE and others have served to show that the threads are composed of one general material, the varying density or alveolation of which may give the appearance of granules.

heterotypic mitosis as representing the two edges of a single alveolated chromosome, and therefore equivalent to the similar paired structures in any somatic prophase. The apparently greater definiteness of the zygonema threads, however, would perhaps indicate that the structures represented in the two cases are not necessarily always the same. Regarding the synaptic pairing she says: "The important point which *Galtonia* demonstrates is that its spirem is univalent. Whether these univalent strands join with their homologous pairs telosynaptically or parasynaptically, or by any other intermediate method between these two extremes, resolves itself merely into a question of non-essential detail." Since *Galtonia* is a form having both long and short chromosomes, this perhaps accounts for the great variety observed in the method of pairing. Possibly if the individual chromosomes can be followed it may be found that the longer ones are more likely to pair parasynaptically and the short ones telosynaptically.

Others, for example OVERTON (17), have suggested that even though there is no exchange of bodies between the paired threads of the presynapsis, yet the purpose of this pairing may be to bring the threads within each other's "influence." A little reflection, I think, will show the futility of this idea. In *Oenothera* the nuclei of the pollen mother cells have an average diameter of less than 10μ . The diameter of the presynaptic threads may be taken to be not more than 0.27μ . Supposing the presynaptic threads to come to lie within their own diameter of each other, it is not clear what chemical or other "influence" could be exerted at the latter distance, which could not be exerted at the former. When it is considered that the chromosomes of the synaptic nuclei have, in higher plants, gone through hundreds of thousands of divisions since they were first associated at the time of fertilization, and that between every two divisions were periods in which the chromosomes were in the alveolated and distributed condition of the "resting" nucleus, in which the portions of the reticulum representing each chromosome must come into the most intimate contact, at least at their boundaries; and when it is further considered that during all this time active metabolic interchanges between nucleus and cytoplasm are taking place, the idea that a pairing of chromosomes or threads at synapsis is necessary for an exchange of influences loses its force.

This leads to another series of facts which students of reduction have frequently failed to take sufficiently into account, namely, that in somatic mitoses the homologous chromosomes are in pairs. MONTGOMERY (15) first suggested, in 1901, that in reduction homologous chromosomes of maternal and paternal origin pair. In the following year SUTTON (26) showed that in *Brachystola magna*, in which various shapes of chromosomes occur, those of like shape are paired in the spermatocytes. The same thing has since been shown for many other animals, and also for various plants. In 1905 STRASBURGER (24) found that this paired condition is not confined to the heterotypic or synaptic chromosomes, but occurs also in the somatic tissues. This was shown by studies of *Galtonia* and *Funkia*, in which the chromosomes are heteromorphic,

being of different lengths. The same thing has since been found to be the case in several other plants having morphological differences in their chromosome group. GEERTS (9) published two figures indicating that in *Oenothera*, in which the chromosomes exhibit no morphological differences (that is, are isomorphic), they are also in pairs in the somatic tissues. Two figures (9 and 10) in a subsequent paper of mine (GATES 5) show indications of the same thing. Therefore, though this cannot be so clearly demonstrated in organisms whose chromosomes are isomorphic, yet it cannot be doubted that the chromosomes are in homologous pairs throughout the somatic cells. OVERTON (17) gives indications of this in *Thalictrum* (pl. 1, fig. 1), and believes (p. 45) that the homologous parental elements are finally brought side-by-side in the somatic nuclei. CLEMENS MÜLLER (16) has recently given a particularly clear demonstration of this paired arrangement, from studies on the root tips of *Yucca* species, in which the chromosomes are either very long or very short.

From these results it is evident that the pairing of homologous chromosomes is not brought about at synapsis or any other period of meiosis, but that the chromosomes are really paired throughout the life cycle of the sporophyte. The pairing must therefore have taken place at the time of fertilization. One of the best contributions that could be made to the study of the life cycle would be the determination of just how the two single sets of x chromosomes in the egg and sperm nuclei become, in the nuclei descended from the fertilized egg, a set of $2x$ chromosomes arranged in homologous pairs. The idea that the final act of fertilization, that is, the pairing of homologous chromosomes, is deferred until synapsis, an idea which has been often expressed, is therefore a mistaken one, and views of synapsis and its importance in the life cycle will have to be modified accordingly. The view that the function of synapsis is to bring about a pairing of chromosomes or of spirems is no longer justified, (1) because the chromosomes are now known to be paired throughout the somatic tissues of the sporophyte, (2) because there is no satisfactory evidence of a smaller unit of structure within the chromosomes whose union or exchange could be brought about if the materials were stretched out into slender

parallel threads, and (3) because even if there were such units they would have an equally good or even better opportunity for interchange during the alveolated reticulum stage which always intervenes between somatic mitoses.

From this point of view, the life cycle of any sexual plant or animal (with reservations for the Ascomycetes and other groups where peculiar conditions of sexuality occur) may be outlined as follows: At or soon after fertilization, the materials composing the sets of chromosomes of the egg and sperm nuclei become arranged in pairs, so that in subsequent mitoses throughout the sporophyte or soma they always reappear as pairs of homologous chromosomes, the members of which originated respectively from the egg and the sperm or male cell. Synapsis plays no special part in the pairing, and indeed appears occasionally to be omitted in some forms.⁵ Meiosis or reduction consists essentially in the segregation of the members of these pairs which have been in association since soon after fertilization. This segregation is followed immediately by what is essentially another mitosis. The gametophytic or germ cell nuclei may then continue to divide with the haploid number of chromosomes until the diploid number is restored by fertilization. The chromosomes are therefore in pairs from the time of fertilization onward, and the members of the pairs are merely segregated in the heterotypic mitosis. The completion of the act of fertilization is not deferred until synapsis, but takes place probably soon after the union of the sexual nuclei; and throughout the sporophyte or soma the chromosomes maintain, to some extent, their relative space relations with each other.

This leaves several obvious points unexplained. Why are there almost universally *two* meiotic divisions without a growth period of the chromosomes between them? The conception of

⁵ GRÉGOIRE (12, p. 332) says regarding synapsis: "Le ramassement synaptique ne peut avoir, par lui-même, aucun rôle à jouer dans l'accomplissement des phénomènes de réduction, mais doit être considéré plutôt comme une conséquence des phénomènes essentiels qui se déroulent dans le noyau. Cela résulte de ce que, dans certains objets, on ne retrouve pas le ramassement synaptique (SCHREINER, JANSSENS, DETON) et que néanmoins les stades leptotènes, pachytènes (et même zygotènes) y montrent une évolution absolument identique à celle que l'on constate dans les objets où se manifeste un ramassement."

BOVERI (1) answers this question. After each mitosis, the chromosomes, and also the nuclei and cytoplasm, must grow before they divide again. Otherwise they will all continue to diminish in size. In tissues whose cells are of approximately equal size, the chromosomes must grow to their original size after each mitosis. At the beginning of meiosis, the chromosomes undergo the usual growth, so that, although the individuals are separated into two groups in the heterotypic mitosis, they must still divide again immediately before they are in condition to undergo further growth. GRÉGOIRE (12, p. 383) therefore suggests that the heterotypic mitosis is a process of chromosome separation intercalated between the last and the next to the last division of the diploid generation.

If the mere separation of the chromosomes whose ancestors have been in close association throughout the sporophyte is the function of meiosis, then the peculiarly characteristic phenomena of synapsis are without an explanation. In a paper on reduction in *Oenothera* (4), I referred to the size relationships of the cells and nuclei in the archesporium and the pollen mother cells. It was pointed out (p. 5) that the cells and nuclei of the sporogenous tissue continue to grow simultaneously from the size indicated by figs. 1 and 2 to that indicated by fig. 4 of that paper. Then (p. 7) the pollen mother cells cease to grow, while their nuclei continue enlarging. This is shown by comparing figs. 4 and 13. During this later growth of the nuclei, synapsis occurs. In figs. 4-10 of the paper cited, the nuclei are all of similar size and are taken from presynaptic cells in the condition shown by fig. 4. In all the later figures (12-32), which are during or after synapsis, the nucleus is seen to be conspicuously larger. A comparison of fig. 4 with figs. 12 and 13 makes it evident that the synaptic "contraction" is partly only an appearance, due to the sudden growth of the nucleus, that is, an increase in the amount of the karyolymph. Occasional threads remain attached to the nuclear membrane and are drawn outward as the nucleus enlarges (cf. figs. 12 and 13). There is also some contraction, however, as shown by comparing the diameter of the reticular area in figs. 12 and 13 with that of the nucleus in fig. 4. In fig. 15, which represents a typical "synaptic ball," it is also evident that the diameter of this ball is less than that of the

nucleus in fig. 4, and it is equally evident that the threadwork in the synaptic ball is much denser than that in the reticulum of fig. 4. Undoubtedly the most important thing that is going on at this time is a rearrangement of the threads of the reticulum to form the more or less continuous threadwork of synapsis. But similar rearrangements go on in the prophase of every somatic mitosis. The peculiar appearance is given to synapsis, and in some degree to the subsequent stages up to diakinesis, by the enormous growth of the nuclear cavity; but, as already pointed out, there is also a certain amount of contraction as the threads of the reticulum become transformed into those of the synaptic ball. In the paper cited I interpreted synapsis in the ordinary way, as resulting from a contraction, but it is evident that this only partly explains the phenomenon, which is largely due to an increase of the karyolymph, accompanied by a rearrangement, without any growth, of the chromatic threads.⁶ It is to be hoped that future students of reduction will make careful series of measurements, to see whether the same size relationships hold for other forms. In making such measurements it will be necessary to take account of the fact that in the later stages of synapsis the nuclear membrane frequently becomes extremely delicate or practically disappears, allowing the cytoplasm to encroach on the nuclear

⁶ In a conversation with Dr. LAWSON at Brussels during the Botanical Congress, he first suggested to me that the synaptic appearance is due to a growth of the nucleus rather than a contraction of the nuclear contents. He has since kindly sent me an advance proof of his paper (12a), the appearance of which was unfortunately delayed, so that I might make more extended reference to it. In studies of the pollen mother cells of *Smilacina* at the time of synapsis, he finds no contraction whatever of the chromatin. From a series of measurements of the presynaptic and synaptic nuclei in *Oenothera*, I find, as above stated, a slight amount of contraction in the area occupied by the nuclear reticulum (though this probably has no special significance), but a very large growth of the nucleus without a corresponding amount of growth in the cytoplasm. Our results, therefore, are essentially in agreement. LAWSON attributes the growth of the nucleus in the pollen mother cell to the fact that the latter is charged with food materials, which leads to the disappearance of vacuoles from the cytoplasm, and an accumulation of sap within the nuclear cavity. The fact that synapsis is now known to be almost coextensive with sexuality itself, occurring even in *Myxomycetes* (OLIVE), would seem to call for a more general explanation of the phenomenon. Later in the present paper I have suggested the direction in which it seems probable to the writer that the explanation of the nuclear growth without chromatin growth, which causes the synaptic appearance, is to be found.

area. Measurements should therefore be made only on nuclei whose membrane is distinct; and of course where nuclei are cut by the knife, only sections should be measured which pass through their greatest diameter.

The fact that, at the beginning of the so-called synapsis period, a conspicuous growth of the nucleus of the pollen mother cell takes place, without an appreciable growth in the size of the cell, means that there must be at this period a readjustment in the Kern-plasma relation (HERTWIG). In another paper (6) considerable attention was devoted to this matter of the Kernplasma relation in *O. gigas*.

It is known that in all higher plants the pollen mother cells first undergo a large amount of growth, in which the nucleus and cytoplasm share simultaneously. In *Oenothera*, as here stated, and probably also in many other plant and animal forms, the nucleus then undergoes further growth, while the cytoplasm remains stationary. The earlier growth of the nucleus of the pollen mother cell is accompanied by a corresponding growth in its chromatic content, so that the reticulum continues to fill the nuclear cavity; but its later growth is due merely to an increase in the karyolymph, while the amount of chromatin ceases to grow, and the reticulum therefore ceases to occupy the whole of the nuclear cavity. During this later nuclear expansion, the chromatin begins the series of rearrangements which change the reticulum to the spirem condition and finally to diakinesis, and which do not necessarily differ in any fundamental particular from the prophases of any somatic mitosis. The peculiar appearances at this time, as compared with somatic prophases, are partly the result of the fact that the rearrangements go on in a much larger cavity, which allows the chromatic materials to be more loosely distributed; while the peculiarities of the diakinesis and the heterotypic gemini may be partly accounted for by the fact that the members of the pairs, instead of lying parallel, usually occupy a great variety of positions relative to each other. Furthermore, in many forms the attraction between homologous chromosomes is probably greater at this time than in somatic mitoses, for the heterotypic gemini are often more closely paired than the chromosomes during the sporophytic divisions.

However, this is not invariably true, and I have shown that in *Oenothera Lamarckiana* and its mutants, and in *O. biennis* (4 and 5, p. 183), the diakinetid chromosomes are usually very loosely paired, owing to a weak attraction between homologous chromosomes.⁷ In *O. grandiflora*, as I have already pointed out (7), the figures of DAVIS (2) indicate that this attraction is greater than in the other forms.

It is not to be supposed that these suggestions offer a full explanation of all the phenomena, but they deserve to be carefully tested in future studies of synapsis. The nuclear enlargement unaccompanied by cytoplasmic growth is probably connected with the fact that two subsequent mitoses, without further chromatin growth, follow each other.

A recent paper by STOMPS (21), on reduction in *Spinacia*, offers some particularly accurate figures of the presynaptic stages (pl. 1, figs. 7-13), drawings of which have been so frequently more or less diagrammatic. STOMPS finds that the chromosomes are never joined to form a continuous spirem, but that their free ends can always be determined. There are 12 somatic chromosomes in *Spinacia*, and in the presynaptic nuclear reticulum STOMPS believes he is able to determine definitely 6 elongated threadlike darker-staining bodies, which are not joined end-to-end, but variously arranged. Each of these bodies is considered to be composed of two longitudinal portions more or less completely fused, which are interpreted as representing two chromosomes laterally paired. These threads are so delicate that interpretations are extremely difficult, so that the correctness of this interpretation must depend upon the accurate demonstration of the number of these bodies. In later stages the threads are very much shorter and thicker, but the figures (pl. 2, figs. 6-13) do not form a close enough series to show whether the final chromosome bivalents are formed by a longitudinal or a transverse segmentation of the 6 (?) bodies represented in the presynaptic stages. If the author's

⁷ In December 1908, in a paper read before the Botanical Society of America (Further studies of *Oenotheran* cytology; abstract in *Science* 29:269. 1909), I showed that the phenomena of reduction in *O. biennis* and in *O. laevifolia* agree in every detail with my earlier account (4) of that process in *O. Lamarckiana* and its mutants.

interpretation is correct, then we have here, somewhat as in ROSENBERG's account for *Drosera*, a lateral pairing of long thread-like chromosomes, which afterward by contraction become short and thick.

It has sometimes been urged as an argument for the parasynaptic method of reduction, that the chromosomes are in pairs side-by-side in the somatic mitoses. When, as is very generally the case in somatic mitoses, the long axis of the chromosomes is several times their short axis, then for mechanical reasons, if they are to continue to keep together in pairs, they will naturally lie side-by-side in the crowded somatic nuclear prophase and metaphase. The same is true of *Oenothera* (as already referred to in this paper), in which the somatic chromosomes are from three to six times longer than broad. They are paired side-by-side in the equatorial plate of somatic divisions. It is not yet known whether in prophase they lie paired side-by-side or end-to-end on a spirem, though the latter is probably the case. But in any case, they are clearly arranged end-to-end in the stages of reduction preceding diakinesis, though after the looped and folded chain segments, they frequently come to lie paired side-by-side. Such pairs, as I have pointed out in previous papers, are almost invariably joined by a linin connection at *one* end, showing clearly their manner of origin. This all goes to prove that while both end-to-end and side-by-side pairings of chromosomes occur, yet no great significance attaches to the difference. In the case of the heteromorphic chromosomes figured by C. MÜLLER (16) in root tips of *Yucca*, the long chromosomes lie in pairs side-by-side, but in the practically globular chromosomes both axes are of the same length, and the distinction between a lateral or endwise pairing breaks down.

Miss STEVENS (20) has shown that in one of the mosquitoes (*Culex*) "parasynapsis of homologous chromosomes often changes to telosynapsis in the metaphase of the first spermatocyte." She says (p. 216): "It is of especial interest to see in *Culex* a perfectly clear case of parasynapsis change in some cases to an equally clear case of telosynapsis before metakinesis, while intermediate ring stages and cases of overlapping ends also occur."

The general point of view resulting from the foregoing studies and considerations may now be briefly stated. Both the telosynaptic and the parasynaptic methods of reduction occur, but the difference is not of phylogenetic significance, depending rather upon the mechanics of nuclear processes. In forms having long threadlike chromosomes, the pairing may be expected to take place side-by-side and a strepsinema stage is therefore likely to occur, while with forms having short stout chromosomes, the pairing is, on account of the different spatial relations, more likely to be end-to-end, the pachynema segmenting directly into a more or less continuous chain of chromosomes. In the same form (for example, in *Oenothera*) the somatic chromosomes may be laterally paired in metakinesis, while the heterotypic gemini are at first arranged end-to-end, later frequently swinging round so as to lie side-by-side. It is probably true, as already pointed out, that the chromosomes in somatic prophase in this genus are also at first arranged endwise. This requires further investigation.

It is also evident that the difference between parasynaptic and telosynaptic pairing in meiosis is devoid of hereditary significance, for reasons already stated. Since the chromosomes are in homologous pairs from the early divisions of the fertilized egg onward, the need for a synaptic contraction to bring about an exchange of particles or influences is imaginary. The synaptic contraction is instead (at least in some forms) in large part an appearance, due to an inordinate increase in the karyolymph at this time. The main established facts regarding the life cycle are that the chromosomes are in homologous pairs throughout the sporophyte, and that the members of the pairs are segregated in the heterotypic mitosis.

I may call attention to the fact that, although reduction consists simply in segregation of the descendants of homologous chromosomes which were first associated as pairs soon after fertilization and remained so associated throughout the sporophyte or soma, yet the orientation of these bodies in the heterotypic metakinesis permits varying distributions of the respective mater-

nal and paternal chromosomes during reduction. This is of particular interest from the standpoint of hybrids, but will not be discussed further in this connection.

A striking proof that a redistribution of characters occurs in sexual but not in asexual or vegetative reproduction is to be found in the case of potatoes. The recent experiments of EAST (3) and of SALAMAN (19) show that potato varieties grown year after year from tubers usually continue true. But when the flowers are self-pollinated the first generation of offspring may show plants of different types. Thus a race of potato with red tubers may on self-pollination produce sexual offspring some of which bear only red tubers and others only white. Here is direct evidence that a segregation and redistribution takes place in sexual reproduction which is absent in vegetative reproduction, or occurs only in the rare cases of "bud sports," through the loss of a character.

The chances for chromosome redistribution during the process of segregation in the heterotypic metaphase certainly furnish the most probable basis for this segregation and redistribution of characters. But as I have pointed out elsewhere (8, p. 211) from the evidence of hybrids, this redistribution of characters must also occur in certain cases at other points in the life cycle.

Summary

Studies of chromosome reduction in different plants indicate that there are two general methods of reduction in organisms, one involving a telosynapsis or end-to-end arrangement of the chromosomes, the other involving a parasynapsis or side-by-side pairing. The difference, however, is not of phylogenetic significance, because both methods may occur in different genera of the same family; nor is it of hereditary significance, because the whole chromosome must be regarded as the unit of nuclear morphological structure.

In general, genera having short chromosomes will show telosynaptic pairing, while in forms with long threadlike chromosomes the chromosomes are likely to pair parasynaptically. In organisms having heteromorphic chromosomes, both methods of pairing may occur in the same nucleus. Whether the pairing shall be end-to-end or side-by-side is therefore not of phylogenetic or hereditary

importance, but is merely a matter of cell mechanics; and the two methods of chromosome reduction are therefore essentially one.

While the behavior of the chromosomes affords abundant evidence of some type of individuality or genetic continuity, yet there is no satisfactory evidence of any smaller unit of structure within the chromosome, and for this and other reasons there can be no hereditary difference between a parasynaptic and a telosynaptic pairing of chromosomes.

The one essential and probably almost universal fact of meiosis or reduction in sexual organisms is the segregation of whole somatic homologous chromosomes in the heterotypic mitosis. The reduction process is everywhere the same in involving a segregation of the somatic chromosomes in the heterotypic mitosis, and a split of these chromosomes in the homotypic.

Since it is now known that the chromosomes are in homologous pairs throughout the tissues of the sporophyte, this pairing must take place soon after the association in the fertilized egg of the two sets of chromosomes derived respectively from the egg and sperm nuclei.

The fact that these homologous chromosomes are closely associated in pairs throughout the sporophyte, deprives synapsis of its supposed function of bringing about an interchange of materials or "influences" just before the chromosomes finally separate.

If, as seems evident, the essential fact of meiosis is the mere segregation and redistribution of the chromosomes whose ancestors have been associated in pairs throughout the sporophyte, then the phenomena of the heterotypic prophase do not differ essentially from those of any somatic prophase.

The unique condition of synapsis or synizesis is considered to be due, in some forms at least (for example, in *Oenothera*), to a sudden growth in the nucleus of the pollen mother cell without corresponding growth of the cytoplasm or of the nuclear reticulum. There appears also to be some contraction of the chromatic threads in the nucleus at this time, but the most important change is a rearrangement of the threads from the reticular to the spirem condition.

The conspicuous appearance of "emptiness" of the synaptic

nucleus is largely due to its sudden expansion by an increase in the karyolymph. This involves a sudden change in the karyoplasmic relation, which is probably connected with the fact that, without further chromatic or cytoplasmic growth, two mitoses, one of which involves a segregation and the other a split of the chromosomes, take place in quick succession.

Synapsis, therefore, has no special significance in the life cycle, but depends upon a temporary change in the karyoplasmic relation, which is necessitated by the segregation process, intercalated between two mitoses, one of which (in plants) is sporophytic and the other gametophytic.

Since the life cycle involves a pairing of homologous chromosomes at the time of fertilization and their continued association in pairs until they are separated in the heterotypic mitosis, synapsis is not the delayed and final act of fertilization, as frequently interpreted. Conceptions of synapsis as bringing about an interchange of chromomeres or particles in the chromosomes are not supported by critical observations; and ideas involving an exchange of "influences" are rendered superfluous by the fact that the homologous chromosomes are paired throughout the sporophyte.

Reduction does not consist in a transverse or qualitative and a longitudinal or quantitative split of the chromosomes according to the conception of WEISMANN, but involves merely a segregation and redistribution of the members of homologous pairs of whole somatic chromosomes. If the most widely accepted general account of reduction be universal, then a transverse segmentation of the chromosomes never regularly occurs. But it may be for purely physical reasons that a somatic chromosome always splits longitudinally. It is not necessary to assume that the function of this split is to produce an equal division and distribution of differentiated "ids" arranged along its axis.

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FILICES WILSONIANAE

H. CHRIST

(WITH TWO FIGURES)

[The ferns collected by Mr. E. H. WILSON from 1907-1908 in Hupeh and Szech'uan, during the Arnold Arboretum expedition to western China, were placed in the hands of Dr. H. CHRIST of Basel. His report upon them is found in the following paper.—C. S. SARGENT, *Arnold Arboretum*.]

Province of Hupeh¹

WOODSIA POLYSTICHOIDES Eat.—Fang Hsien; cliffs, 4000-6000 ft.; August 1907; no. 2602.—J.

DRYOPTERIS DECURSIVE-PINNATA (*Polypodium* Van Hall) O. Ktze.—Patung Hsien; woodlands, 3000-4000 ft.; May 1907; no. 2599.—J.

DRYOPTERIS ROBERTIANA (*Polypodium* Hoffm.) C. Chr. Ind.—Fang Hsien; cliffs, 4000-6000 ft.; August 1907; no. 2627.—E.A.

DRYOPTERIS HENDERSONI (*Lastrea* Bedd.) C. Chr. Ind. (*Aspidium spectabile* Wall.).—Changyang Hsien; woodlands, 3000-4000 ft.; May 1907; no. 2630.—H.

POLYSTICHUM SPECIOSUM (*Aspidium* Don) J. Sm. (*Aspidium affine* Wall.).—Patung Hsien; woods, 1800 ft.; April 1907; no. 2626.—H.

*POLYSTICHUM MUPINENSE (*Aspidium* Franchet) Bedd.—Fang Hsien; cliffs, 4000-6000 ft.; September 1907; no. 2601.

*POLYSTICHUM ICHANGENSE Christ.—Fang Hsien; cliffs, 4000-5000 ft.; August 1907; no. 2609.

POLYSTICHUM ACULEATUM (L.) Schott.—Forma tenera, profunde dentata, caeterum typica.—Hsing-shan Hsien; woods, 4000-6000 ft.; August 1907; no. 2611.—H.J.E.A.

*POLYSTICHUM DEVERSUM Christ, n. sp.—Fang Hsien; woodland, 5000-6000 ft.; August 1907; no. 2625.

¹ I have indicated with an H the species found in India and chiefly on the southern slope of the Himalayan Chain; those found in Japan with a J; those found in Europe with an E; and those found in America with an A. I have indicated with an asterisk (*) the species peculiar to Hupeh and western Szech'uan.

*POLYSTICHUM MOLLICULUM Christ, n. sp.—Fang Hsien; 8000 ft.; June 27, 1907; no. 2657.

*POLYSTICHUM LEUCOCHLAMYS Christ, n. sp.—Fang Hsien; woods, rocks, 5000–6000 ft.; November 1907; no. 2600.

*POLYSTICHUM LOBATUM (*Aspidium* Hds.) Prsl. var. CHINENSE Christ Nuov. Giorn. Bot. Ital. 4:92. 1897, et Bull. Soc. Bot. France 5:1905.—Hsing-shan Hsien; 4000–6000 ft.; July 1907; no. 2612.

POLYSTICHUM DELTODON (*Aspidium* Baker) Diels.—Fang Hsien; woods, 5000–6000 ft.; November 1907; no. 2620.

CYRTOMIUM FALCATUM (*Polypodium* L. fil.) Prsl. var. MUTICUM Christ Notulae System. Mus. Paris no. 25. 1909.—Hsing-shan Hsien; woods, 4000–5000 ft.; August 1907; no. 2628.

ODONTOSORIA CHINENSIS (*Trichomanes* L.) J. Sm.—Ichang; roadsides and sunny places generally, 1000–1400 ft.; July 1907; no. 2663.—H.J.

ASPLENIUM PROLONGATUM Hook.—Fang Hsien; rocks, 1000–1500 ft.; August 1907; no. 2655.—H.J.

ASPLENIUM TRICHOMANES L.—Fang Hsien; cliffs, 4000–7000 ft.; August 1907; no. 2659.—H.J.E.A.

BLECHNUM EBURNEUM Christ.—Patung Hsien; moist cliffs, 2000 ft.; July 1907; no. 2678.

CONIOGRAMME FRAXINEA (*Diplazium* Don) Diels.—Fang Hsien; woodland; November 1907; no. 2679.—H.J.

ADIANTUM PEDATUM L.—Fang Hsien; woods, 3000–6000 ft.; July 1907; no. 2672.—H.J.A.

*ADIANTUM ARISTATUM Christ, n. sp.—Fang Hsien; rocks, 3000–4000 ft.; November 1907; no. 2674.

PTERIDIUM AQUILINUM (L.) Kuhn.—Ichang; abundant (starch is obtained from the rhizome), 1000–10,000 ft.; May 1907; no. 2682.—H.J.E.A.

PTERIS LONGIFOLIA L.—Ichang; dry rocks, 1000–3000 ft.; April 1907; no. 2665.—H.J.E.A.

PTERIS CRETICA L. var. SUBSERRULATA Christ, n. var.—Fang Hsien; shady rocks; July 1907; no. 2670.

POLYPODIUM SUBAMOENUM Clarke.—Fang Hsien; 4000–6000 ft.; August 1907; no. 2648.—H.

POLYPODIUM CHINENSE Metten.—Fang Hsien; cliffs, rocks, 3000–6000 ft.; August 1907; no. 2640.

POLYPODIUM EXCAVATUM Bory.—Hsing-shan Hsien; rocks, 2000–5000 ft.; August 1907; no. 2635.—H.J.

*POLYPODIUM LINEARE Thunberg.—Hsing-shan Hsien; rocks, 2000–5000 ft.; August 1907; no. 2635 bis.—H.J.

POLYPODIUM CONTORTUM Christ (*P. lineare* Thnbg. var. *contortum* Christ Nuov. Giorn. Bot. Ital. 4:1. Jan. 1897–1898).—Fang Hsien; rocks and trees, 4000–6000 ft.; August 1907; no. 2636.

POLYPODIUM CLATHRATUM Clarke.—Fang Hsien; cliffs, 3000–6000 ft.; August 1907; no. 2642.—H.

POLYPODIUM DRYMOGLOSSOIDES Baker.—Fang Hsien; on trees and rocks, 3000–5000 ft.; July 1907; no. 2647.

DRYMARIA FORTUNEI (*Polypodium* Ktze.) J. Sm.—Ichang; abundant on rocks and trees, 1000–3000 ft.; April 1907; no. 2646.

CYCLOPHORUS CALVATUS (*Polypodium* Baker) C. Chr. Ind. 198.—Fang Hsien; cliffs, 3000–6000 ft.; August 1907; no. 2641.

CYCLOPHORUS DRAKEANUS (*Polypodium* Franchet) C. Chr. Ind. 198.—Fang Hsien; cliffs, 1000–6000 ft.; no. 2627.

LOXOGRAMMA INVOLUTA (*Grammitis* Don) Presl. (*Polypodium scolopendrinum* C. Chr. Ind. 562).—Hsing-shan Hsien; 2000–5000 ft.; October 1907; no. 2661.—H.

GLEICHENIA LINEARIS Burm.—Ichang; open country, forming jungles, 1000–3000 ft.; no. 2677.—H.J.A.

OSMUNDA REGALIS L.—Patung Hsien; grassy spots, ravines, etc., 1000–5000 ft.; May 1907; no. 2676.—H.J.E.A.

LYCOPODIUM CLAVATUM L.—Patung Hsien; grassy spots, 5000–6000 ft.; July 1907; no. 2656.—H.J.E.A.

LYCOPODIUM OBSCURUM L.—Fang Hsien; rocks in silver fir forests, 9500 ft.; May 16, 1907; no. 2650.—J.A.

SELAGINELLA CAULESCENS Spring.—Ichang; glen, 1–1000 ft.; May 1907; no. 2654.—H.J.

Province of Szech'uan

HYMENOPHYLLUM BLUMEANUM Spreng.—Mupin; wet rocks, woodland, 4000–6000 ft., August 1908; no. 2681.—H.

WOODSIA DELAVAYI Christ.—Northeast of Ta-t sien-lu; 7200 ft.; July 2, 1908; no. 2616.

DRYOPTERIS CRENATA (*Polypodium* Forskal.) O. Ktze.—Mupin; cliffs, 4000–6000 ft.; August 1908; no. 2631.—H.

DRYOPTERIS MARGINATA (*Aspidium* Wallich Cat. 391).—Mupin; woodland, 4000–6000 ft.; August 1908; nos. 2604, 2632.—H.

*DRYOPTERIS PSEUDOCUSPIDATA Christ, n. sp.—Mupin; woodland, 6000 ft.; August 1908; no. 2603.

DRYOPTERIS DECURSIVE-PINNATA (*Polypodium* Van Hall) O. Ktze.—Mupin; woodland, 4000–6000 ft.; August 1908; no. 2618.—J.

POLYSTICHUM PRESCOTTIANUM (*Aspidium* Wallich) Moore.—Ta-tsien-lu; woods, 6000 ft.; June 1908; no. 2622.—H.

*POLYSTICHUM MUPINENSE (*Aspidium* Franchet) Bedd.—Mupin; rocks in woods, 4000–6000 ft.; August 1908; no. 2617.

*POLYSTICHUM OTOPHORUM (*Aspidium* Franchet) Bedd.—Mupin; cliffs, 5000–6000 ft.; August 1908; nos. 2598, 2624.

*POLYSTICHUM WILSONI Christ, n. sp.—Mupin; woodland, 4000–6000 ft.; August 1908; no. 2614.

*POLYSTICHUM WOODSIOIDES Christ, n. sp.—Mupin; woodland, 4000–6000 ft.; August 1908; no. 2615.

*POLYSTICHUM LACERUM Christ, n. sp.—Mupin; rocks, 4000–6000 ft.; August 1908; no. 2608.

*POLYSTICHUM LEUCOCHLAMYS Christ, n. sp.—Mupin; rocks, 4000–6000 ft.; August 1908; no. 2606.

POLYSTICHUM STENOPHYLLUM Christ.—Mupin; cliffs, 4000–6000 ft.; August 1908; no. 2618.

POLYSTICHUM THOMSONI (*Aspidium* Hook. fil.) Bedd.—Mupin; woodland, 4000–6000 ft.; August 1908; no. 2607.—H.

POLYSTICHUM CARVIFOLIUM (*Aspidium* Ktze.) C. Chr. Ind.—Mupin; woodland, 4000–6000 ft.; August 1908; no. 2605.—H.J.

SOROLEPIDIUM GLACIALE (*Polystichum* Christ) Christ, n. gen.—Mupin; cliffs, 5000 ft.; August 1908; no. 2613.

CYRTOMIUM LONCHITOIDES Christ.—Mupin; cliffs, 5000–6000 ft.; August 1908; nos. 2621, 2623.

DAVALLIA ATHAMANTICA Christ.—Mupin; cliffs, 4000–6000 ft.; August 1908; No. 2666.

LINDSAYA CULTRATA Sw.—Mupin; cliffs, 4000–6000 ft.; August 1908; no. 2671.

ATHYRIUM NIGRIPES Blume.—Mupin; rocks, 4000–6000 ft.; August 1908; no. 2660.—H.J.

ATHYRIUM PYCNOSORUM Christ.—Mupin; 4000–6000 ft.; August 1908; no. 2656.—J.

*ATHYRIUM MUPINENSE Christ, n. sp.—Mupin; woodland, 4000–6000 ft.; August 1908; no. 2610.

ASPLENIUM PRAEMORSUM Sw.—Mupin; cliffs, 4000–6000 ft.; August 1908; no. 2662.—H.A.

ASPLENIUM YUNNANENSE Franchet.—Mupin; cliffs, 4000–6000 ft.; August 1908; no. 2658

BLECHNUM EBURNEUM Christ.—Mupin; wet rocks, 3000–5500 ft.; August 1908; no. 2678.

GYMNOPTERIS VESTITA (*Grammitis* Wallich).—Northeast of Ta-tsien-lu; dry banks, 7000 ft.; February 7, 1908; no. 2668.—H.

*GYMNOPTERIS SARGENTII Christ, n. sp.—Monkong Ting; loamy places, warm valleys, 7000–9000 ft.; June 28, 1908; no. 2669.

PELLAEA NITIDULA (*Pteris* Wallich) Baker.—Northeast of Ta-tsien-lu; dry rocks, 6900–8000 ft.; June 30, 1908; no. 2664.—H.

DORYOPTERIS DUCLOUXII Christ.—Mupin; loamy banks, old walls, etc., 3000–5000 ft.; August 1908; no. 2667.

ADIANTUM PEDATUM L.—Mupin; woodland, 4000–6000 ft.; August 1908; no. 2673.—H.J.A.

ADIANTUM VENUSTUM Don.—Mupin; rocks in wood, 4000–5000 ft.; August 1908; no. 2675.—H.

PLAGIOGYRIA ADNATA (*Lomaria* Blume) Bedd.—Hung Yah Hsien; 3000 ft.; September 8, 1908; no. 2680.—H.J.

VITTARIA SUBEROSA Christ.—Wa-shan; on trees and rocks, 5000–7000 ft.; September 1908; no. 2638.

POLYPODIUM SUBAMOENUM Clarke.—Mupin; rocks, 3000–6000 ft.; August 1908; no. 2648.—H.

*POLYPODIUM TALIENSE Christ.—Mupin; rocks, 3000–6000 ft.; August 1908; no. 2649.

POLYPODIUM ANNUIFRONS Makino.—Ta-tsien-lu; rocks in wood, 6000–8000 ft.; June 1908; no. 2637.—J.

POLYPODIUM ENGLERI Luer ss.—Mupin; cliffs, 4000–7000 ft.; August 1908; no. 2639.—J.

POLYPODIUM SHENSIENSE Christ.—Mupin; cliffs, 4000–6000 ft.; August 1908; no. 2644.

POLYPODIUM LEHMANNI Metten.—Mupin; woodland, 4000–6000 ft.; August 1908; no. 2643.—H.

POLYPODIUM GRIFFITHIANUM Hook.—Mupin; 4000–6000 ft.; August 1908; no. 2645.—H.

POLYPODIUM LINEARE Thunbg.—Ta-tsien-lu; on trees, 4000–8000 ft.; June 1908; no. 2633; on rocks, no. 2634.—H.J.

LYCOPodium LUCIDULUM Michaux.—Northeast of Ta-tsien-lu; rocks, 8000–10,000 ft.; June 1908; no. 2651.—H.A.

Diagnoses of the new species

Sorolepidium H. Christ, genus novum.—Habitu *Ceterach*, characteribus potius *Polystichum* referens, differt soris magnis medialibus in nervulo basali anteriore nervorum lateralium terminalibus, subrotundis, indusio proprio deficiente, indusio spurio squamis singulis vel duabus aut tribus subulatis et fimbriatis e basi receptaculi oriundis constituto.

This beautiful plant, which much resembles a xerophilous alpine Tibetan species, deserves as well as *Plecosorus* to be separated from *Polystichum* by the characters indicated above. The indusial scales are found at the base of the receptacle and are inserted on the vein, arising at the base of the pedicels of the sporangia. There is always one larger scale, and sometimes one or two smaller ones; and also always a very large one inserted on the costa of the pinna and covering the sorus. FRANCHET has placed this plant with *Gymnogramme* in the Paris Herbarium, without naming it, probably because of the confluent sori without indusia; but the sorus does not follow the soriferous vein longitudinally as in *Gymnogramme*, it is attached to a terminal receptacle.

Sorolepidium glaciale (*Polystichum* Christ Foug. de la Chine Mus. Hist. Nat. Paris, Bull. Soc. Bot. France IV. 5:28), fig. 1.

HAB.—Seems widely distributed in the high ranges of western China.

Discovered by Abbé DELAVAY in Yunnan on rocky declivities at the foot of the Lu Kiang glacier, July 9, 1884, n. 45. Herb. Paris. Rediscovered by WILSON in the western part of Szech'uan, 1903–1904, no. 537 (Herb. James Veitch & Sons), Bull. Acad. Geog. Bot. Mans 110, 1906; by the same collector

in the same region, Mupin, cliffs 5000 ft., August 1908, no. 2613 (Herb. Harvard Univ.).

I owe to the kindness of Mademoiselle CHARLOTTE TERNETZ, Ph.D., of Basel, the drawings of the enlarged details of this plant.

Polystichum leucochlamys H. Christ, n. sp.—Rhizomate brevi, pollicis crassitie, radicoso, cum stipite rachique squamis magnis patentibus ovato-acuminatis 4 mm. longis brunneis longe fimbriato-ciliatis, in rachi sensim diminutis et angustatis, fasciculatis et lacertis tecto; foliis fasciculatis, stipite 8–12 cm. longo, viridi aut stramineo 2 mm. crasso. Lamina lanceolato-caudata, ad basin angustata, rachi debili et arcuata praedita, 30 cm. longa 4.5 cm. lata, apice nuda elongata et gemma vivipara instructa, pinnata, pinnis 30–40 utrinque, approximatis sive admodum distantibus, infimis diminutis et reflexis, caeteris patentibus lanceolato-falcatis obtusis rarius acutis, subsessilibus, 2 cm. longis, basi 0.5 cm. latis, basi inaequalibus, postice cuneatis, antice acute auriculatis, crenatis aut decumbentiserratis, nervis valde obliquis, soris rotundis, marginalibus, uniseriatis margini anteriori insertis, indusiis maximis, 2 mm. diametro, scarioso-hyalinis, imbricatis, bullatis, albidis, diaphanis, umbilicatis, margine minu-



FIG. 1.—*Sorolepidium glaciale* Christ: a, larger pinnule, showing circular attachment of sorus (somewhat too strongly marked), $\times 5$; b, portion of a pinnule (x, end of sorus nervule; y, the sporangium stalks still remaining; z, sorus with overlying scale from principal nerve and the under scale arising from sorus nerve), $\times 15$; c, large scale, $\times 10$; d, small scale, $\times 10$.

tissime fimbriato. Faciebus hinc inde setulosis. Textura herbacea, colore dilute viridi.

Facie *P. auriculati* (L.) Prsl., characteribus *P. craspedosori*.

Highly developed form of the type of *P. craspedosorum* (*Aspidium* Maxim.) Diels; distinguished by larger dimensions, elongated stipe, and very broad swollen scarious white indusia. It is surprising to see this species from two localities so widely separated as W. Hupeh and W. Szech'uan.

HAB.—Rocky places, Mupin, W. Szech'uan, 4000–6000 ft., August 1908, no. 2606; woods and rocks, Fang Hsien, W. Hupeh, 5000–6000 ft., November 1907, no. 2600.

Polystichum lacerum H. Christ, n. sp.—Rhizomate brevi, squamis brunneis lanceolato-acuminatis 3 mm. longis fimbriato-ciliatis vestito, foliis coespitoso-fasciculatis numerosis (12) stipite brevi 3–4 cm. longo, stramineo, sed iisdem squamis setulisque cum rachi abunde tecto, lamina 12–15 cm. longa 22 cm. lata lanceolata versus apicem acuminata breviter caudata et gemma minima saepius abortiva terminata, versus basin vix angustata, pinnata, sed pinnis infimis basi profunde et fere ad costam incisis, pinnis ca. 25 utrinque patentibus, inferioribus suboppositis, sessilibus, 1 cm. longis basi 1.5 cm. latis cuneato-ovatis falcatis acutis, basi inaequalibus i.e., antice valde auriculatis, profunde lobatis, lobis ca. 5 utrinque, ovato-obtusis, rarius crenulatis. Soris magnis plerumque uniseriatis margini anteriori insertis, brunneis, sese tangentibus et subconfluentibus, indusio 0.5 mm. lato obscure griseo tenuissimo, sporangiis arctissime adhaerente margine lacerato, demum evanescente. Textura herbacea, facie superiore calva obscure viridi, inferiore hirsuta, pallidiore.

HAB.—Rocks, Mupin, 4000–6000 ft., August 1908, no. 2608.

Member of the group of *P. craspedosorum* (Maxim.) Diels, of the same habit, but with pinnae more scaly and more incised, and with the indusium more delicate and fringed.

These three species (*P. leucochlamys*, *P. craspedosorum*, and *P. lacerum*) form a distinct group of *Polystichum* (CRASPEDOSORA), characterized by marginal sori inserted at the anterior border of the pinnae, by a broad and membranaceous indusium exceeding the sorus, and by the point of the proliferous rachis. The best developed form of the group is *P. leucochlamys*, the least developed is *P. lacerum*. These two seem peculiar to western and central China, while the intermediate form, *P. craspedosorus*, extends throughout China to Japan and Corea.

Polystichum Wilsoni H. Christ, n. sp.—Rhizomate crasso obliquo radicoso atrobrunneo, squamis magnis ovato-acutis scariosis dilute brunneis margine saepe laceratis 6 mm. longis vestito, stipitibus subfasciculatis, 17 cm. longis, luteo-stramineis, 2 mm. crassis, iisdem squamis sparsis, et insuper cum rachi squamis lanceolato-linearibus et subulatis longis albidis setisque vestitis. Lamina 45 cm. longa 10 cm. lata acuminata, versus basin sensim angustata, pinnis infimis remotis valde abbreviatis et deflexis. Lamina bipinnata, pinnis ca. 35 utrinque alternis sessilibus approximatis, 5 cm. longis basi 16 mm. latis acuminatis, basi subinaequalibus i.e., pinnula basali anteriore reducta, pinnulis confertis ca. 15 utrinque, obliquis, sessilibus, oblongis acutis, inaequalibus, postice minus, antice creberrime et profunde biserrato-aristatis, dentibus angustis pectinatis, soris medialibus brunneis confluentibus, indusio inconspicuo fugaci orbiculari minuto, 0.5 mm. lato nigro-umbonato. Facie superiore pilis longissimis lucentibus parce, facie inferiore cum costa costulisque setis longis subulatis albican- tibus pilisque abunde vestita. Textura herbacea, colore luteo- virente.

HAB.—Woodlands, Mupin, 4000–6000 ft., August 1908, no. 2614.

Inter *P. aculeatum* (*Polypodium* L.) Schott et *P. Bakerianum* (*Aspidium* Atkins.) Diels intermedium.

Polystichum deversum H. Christ, n. sp.—Rhizomate brevi erecto, squamis latis ovalibus acutis scariosis brunneis vestito. Stipitibus fasciculatis 4 cm. longis, iisdem squamis et minoribus laceratis vestitis, sulcatis, 1.5 mm. crassis. Lamina 33 cm. longa, 3 cm. lata acuminata, versus basin sensim angustata, lineari-lanceolata, pinnata, rachi straminea, squamis castaneis fasciculatis laceratis variegata, pinnis ca. 45 utrinque, pectinato-confertis, petiolulatis, deflexo-reversis, inaequalibus, 11 mm. longis, basi 6 mm. latis, rhombeo-trigonis, basi posteriore cuneato-abscissis, anteriore acute auriculatis subintegris aut minute crenulatis, nervis confertis ramosis subflabellatis, soris medialibus, remotis, rotundis, ca. 5 utrinque. Facie superiore subglabra, inferiore squamis acutis adpressis ochroleucis tecta, margine breviter ciliato. Textura firme papyracea, colore supra laete virente, subtus pallidiore lutescente.

HAB.—Woodlands, Fang Hsien, W. Hupeh, 5000–6000 ft., August 1907, no. 2625.

Group of *P. deltodon* (Bak.) near *P. stenophyllum* Christ, but distinguished by its larger dimensions, short stiped fronds gradually attenuated toward the base, broad triangular-rhomboidal pinnae hardly dentate and with a dense coating of appressed scales.

Polystichum woodsoides H. Christ, n. sp.—Rhizomate brevi, squamis integris ovatis brunneo-scariosis 3 mm. longis vestito, foliis fasciculato-coespitosis numerosis (10), stipite valido, obeso 1.5 mm. crasso 6 cm. longo flavo-stramineo versus basin atro-brunneo, squamis scariosis dilute brunneis ovatis acutis integris, angustioribus pilisque brevibus mixtis vestito, rachi crassa setulis pallidis pubescente, fronde 15 cm. longa, 23 mm. lata lineari-lanceolata acuminata versus basin angustata, bipinnatifida, pinnis confertis, inferioribus remotioribus et valde diminutis, ca. 27 utrinque, fere sessilibus deltoideo-oblongis, e basi latissima versus apicem obtusum attenuatis, 1 cm. longis, basi 0.5 cm. latis, profunde et ad basin ad costam incisis, segmentis ca. 5 utrinque imbricate-confertis, infimis liberis, superioribus basi connatis, ovatis acutiusculis, minute dentatis, subtus pubescentibus, supra calvis, soris in tertia frondis parte superiore positis, numerosis, 3 aut 4 pro lobo, rotundis, continguis et confluentibus, brunneis, indusio peltato corrugato persistente brunneo minuto, umbone nigro. Textura molliter herbacea, colore supra obscure, subtus pallide virente.

HAB.—Woodlands, Mupin, 4000–6000 ft., August 1908, no. 2615.

Species with very narrow fronds resembling in habit small alpine species of the group of *P. lachenense* (Hook.) Bedd., but belonging rather to the group of *P. mupinense* (Franch.), being bipinnate. Remarkable for the very small but much incised pinnae and thick rachis.

Polystichum molliculum H. Christ, n. sp.—Rhizomate brevissimo radicoso coespitoso, cum stipitis basi squamulis subulatis brevibus sparso. Stipitibus fasciculatis numerosis stramineis filiformibus 3.5 cm. longis, cum rachi raris setulis sparsis, lamina 4 cm. longa, 1 cm. lata, lanceolata obtusa bipinnatifida. Pinnis ca. 4 utrinque suboppositis, sessilibus, late obovatis basi subinaequalibus antice auctis, flabellato-incisis, inferioribus usque ad costam partitis ideoque auriculatis, lobatis, 3 ad 5 mm. longis et

latis, lobis ovato-rotundatis acutis interdum dentatis. Soris magnis, singulis in lobis, demum confluentibus, indusio inconspicuo corrugato. Textura tenuiter herbacea, colore laete virente.

HAB.—Rocks, Fang Hsien, 8000 ft., June 27, 1907, W. Hupeh, no. 2657.

An extremely reduced species, with the habit of a very small *Cystopteris*, distinguished from *P. capillipes* (Baker) Diels by the less incised pinnae with broader segments.

With the six species here described, with which Mr. Wilson has enriched the flora of China, the Chinese species of *Polystichum* now known number 52. There are few examples of so rich and continuous a development without gaps between the different known forms of this genus, so essentially Chinese. The species of *Polystichum* of other regions of the globe seem to be only derivatives or scattered offshoots of this great eastern center.

Gymnopteris Sargentii H. Christ, n. sp.—Rhizomate valido pollicis crassitie, obliquo, setis mollibus 0.5 cm. longis pallide rufis densissime oblecto, radicibus numerosis fasciculatis. Stipitibus subfasciculatis 3 aut 4, flexuosis crassis rigidis 3 mm. diametro, rufo-stramineis, 8 cm. longis, cum rachi aequae rigida et 2 ad 2.5 mm. crassa costisque tomento albido-fulvo omnino-vestitis, lamina late deltoideo-ovata 20 cm. longa 9 cm. lata abunde bipinnata, pinnis remotis ca. 6 utrinque infra apicem brevem simpliciter pinnatum, erecto-patentibus, infimis suboppositis coeteris alternis, basalibus haud abbreviatis, 7 cm. longis 14 mm. latis, lineari-lanceolatis breviter petiolatis, costa rigida vix 1 mm. crassa, pinnulis ca. 7 utrinque, approximatis, deltoideis obtusis basi late trilobo-hastatis 7 mm. longis 5 mm. latis petiolulatis, rigide coriaceis, supra calvis obscure viridibus, subtus et margine densissime rufotomentosis nitidis. Soris submarginalibus confluentibus.

HAB.—Loamy places in warm valleys, Monkong Ting, W. Szech'uan, 7000-9000 ft., June 28, 1908, no. 2669.

This is the most developed species of the series formed by the three species *G. vestita* (*Grammitis* Wallich) Underw., *G. bipinnata* Christ (Notul. Systemat. Mus. Paris no. 2, p. 23. 1909), and *G. Sargentii*, distinguished by its larger dimensions, and a broadly bipinnate frond with numerous trilobed pinnules. Habit nearly that of *Pellaea hastata* (Thnbg.) Prantl. *G. bipinnata* differs by the slender rachis, elongated lanceolate pinnate to nearly bipinnate fronds, and less incised pinnules.

Athyrium mupinense H. Christ, n. sp.—Rhizomate brevi erecto radicoso, cum basi stipitis setis atrobrunneis flexuosis fere

0.5 cm. longis e verruca oriundis vestito. Stipitibus fasciculatis numerosis (ca. 12) tenuibus flaccidis stramineis 5 cm. longis, lamina 20 cm. longa 5.5 cm. lata acuminata basi aliquantulum angustata lanceolato-oblongo bipinnata. Rachi tenui parce setulosa, planta caeterum calva. Pinnis 25-30 utrinque, alternis, approximatis, recte patentibus, deltoideo-ovatis acutis, petiolulatis basi inaequalibus i.e., pinnula basali anteriore aucta, 2 cm. longis basi 12 mm. latis, ad alam angustam incisis, pinnulis confertis sessilibus, infimis rarius subpetiolulatis, ca. 7 utrinque, oblongis subobtusis, basi subinaequalibus i.e., antice auctis, 1 cm. longis 3 mm. latis, acute sed breviter serratis nec aristatis, soris rotundis vix 1 mm. latis brunneis ca. 4 utrinque, medialibus, haud confluentibus, indusio fugaci reniformi. Textura flaccide herbacea, colore obscure virente.

HAB.—Woodland, Mupin, 4000-6000 ft., August 1908, no. 2610.

Affine *A. demisso* Christ in Fedde Repert. 5:284. 1908. Insularum Jezu et Quelpaert, quod differt dentibus aristato-pectinatis. Planta humilis, *A. anisoptero* Christ aut *Cystopteridi* similis.

Adiantum aristatum H. Christ, n. sp.—Rhizomate breviter repente, tenui, squamis subulatis atrobrunneis vestito. Stipite valido, erecto, tereti, atropurpureo nitido, laevi uti tota planta, 1.5 mm. crasso 120 cm. longo. Fronde late deltoideo-ovata, basi rotundata, apice acuta aut obtusa, 13 cm. longa, 9 cm. lata, tripinnata, pinnis pinnulisque imbricato-confertis, brevissime petiolatis, pinnis 6-10 atrinque curvato-ascendentibus inferioribus, deltoideo-ovatis, 8 cm. longis, pinnula basali anteriore rachi incumbente, segmentis latissime cuneato-flabellatis, antice semicircularibus, 1 cm. latis, 8 mm. longis, papyraceo-firmulis, glauco-viridibus, antice profunde et creberrime aristato-serratis, dentibus deltoideis, dentibus usque ad ca. 24 numero. Nervis confertis flabellatis. Soris numerosis sed medio in margine segmenti solitariis rarissime binis i.e., partitis, usque ad 2 mm. longis 1.5 mm. latis, leviter curvatis nec sinu inclusis, indusio ochraceo firmo laevi.

HAB.—Rocks, W. Hupeh, Fang Hsien, 3000-4000 ft., November 1907, no. 2674.

Of the group of *A. venustum* Don, which is essentially Chinese (DIELS Fl. Central China 5:201. 1901), and which embraces half a score of species

related but perfectly distinct; two species extend beyond China, *A. venustum* of northern India and *A. monochlamys* Eaton of Japan. Our species is nearest to *A. Davidi* Franch., but differs in its larger dimensions, more rounded, monosorous pinnules, with numerous and aristate teeth.

Dryopteris pseudocuspidata H. Christ, n. sp.—Rhizomate repente, fere digiti minoris crassitie, brunneo, sublaevi, radicoso, stipite subsolitario, anguloso, 55 cm. longo, sublucido, dilute brunneo, pennae cygni crassitie, versus basin squamis ovatis obtusis brunneis deciduis sparso, planta caeterum laevi. Fronde 36 cm. longa 22 cm. lata, basi haud angustata, late ovato-deltoides, acuminata, pinnata, pinnis ca. 18 utrinque, patentibus, 12 cm. longis 1.5 cm. latis lanceolato-acuminatis, vix petiolulatis, basi rotundato-truncatis, superioribus sensim diminutis nec adnatis, suprema petiolata valde diminuta. Pinnis dentatis, dentibus decumbentibus acutis interdum serrulatis. Costa manifesta prominente. Nervis ca. 40 utrinque, patentibus. Nervulis plerumque 6 utrinque, omnibus arcu acuto junctis. Soris minutis 6 utrinque medialibus brunneis, rotundis, separatis, exindusiatis. Textura papyracea, colore opaco, obscure viridi.

HAB.—W. Szech'uan, woodland, Mupin, 6000 ft., August 1908, no. 2603.

Habit of *D. cuspidata* (*Aspidium* Metten.) syn. *D. khasiana* C. Chr. Ind. 272, but belonging to the group *Nephrodium* with six lateral united veinlets.

PTERIS CRETICA L. var. **subserrulata** H. Christ, n. var.—A typo differt foliis papyraceis nec subcoriaceis dimorphis, fertilibus valde angustatis, sterilibus magis compositis, pinnis inferioribus basi bi- aut tripartitis, pinnulis lateralibus abbreviatis, rachi superiore late alata, marginibus acute et grosse biserratis.

HAB.—Shady rocks, Fang Hsien, 3000–5000 ft., July 1907, no. 2670.

In China *P. cretica* varies much and approaches *P. serrulata* L. fil. There are also forms of the latter species that approach *P. cretica* (Filic. Shen-si septentr. a P. J. GIRALDI lectae in Nuov. Giorn. Bot. Ital. IV. 1:6. 1897; *Pteris serrulata* var. *intermedia* Chr.), so that it is sometimes difficult to maintain a difference between the two species.

The starch of *Pteridium aquilinum* (L. Kuhn)

The specimen of starch from the rhizome of *Pteridium* from Ichang, below the famous gorge of the upper Yang-tze, Province Hupeh, that Mr. E. H. WILSON sent to Harvard University, con-

sists of compact angular fragments 1 cm. or more square, very white and pure, derived evidently from a layer precipitated in water. Professor SENN of Basel has kindly examined the specimen and I owe to him the accompanying drawings and the following description:

“The starch in question consists for the most part of combined grains. The grains joined in pairs have one side parabolically

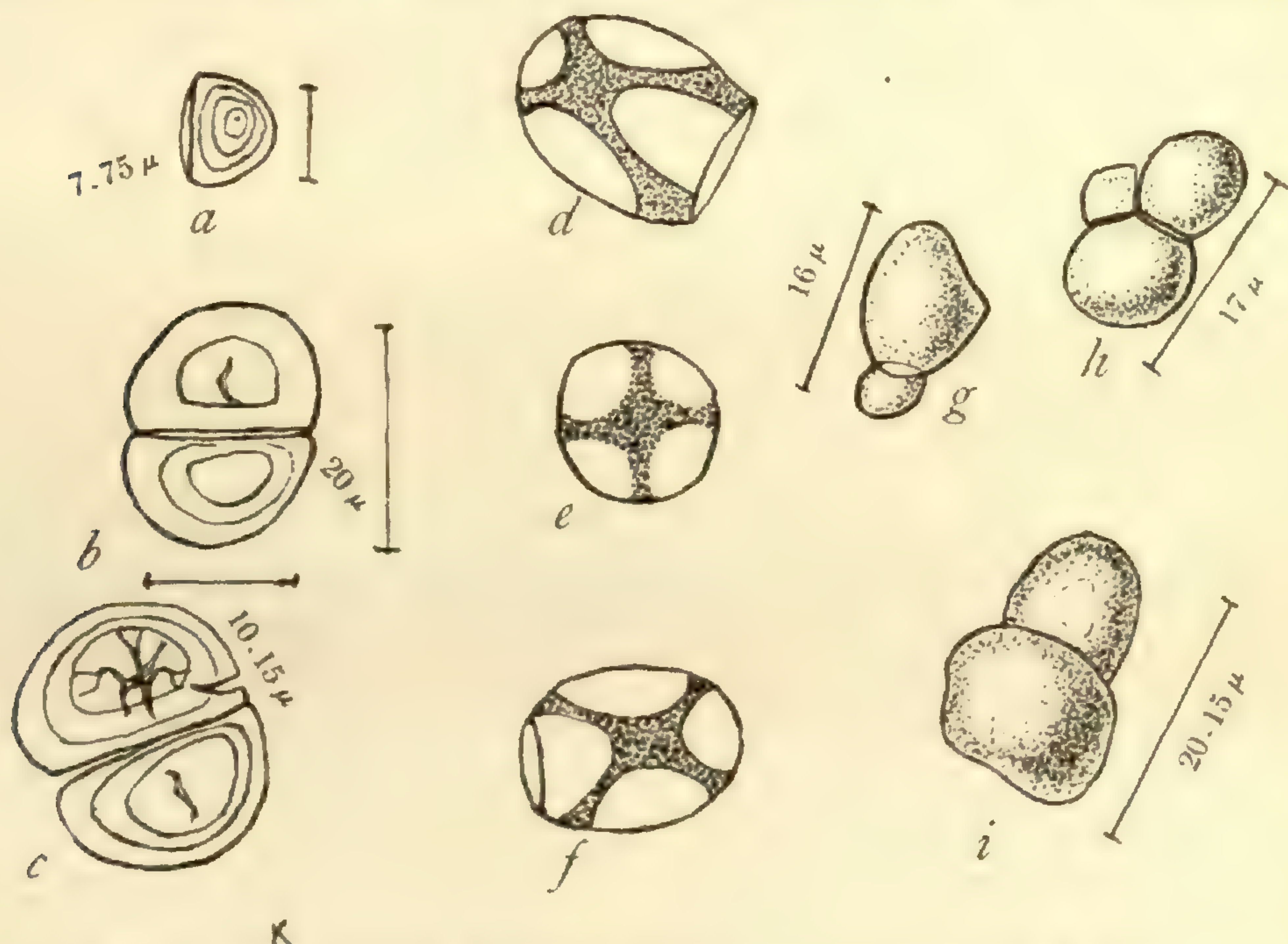


FIG. 2.—Starch of *Pteridium aquilinum*: explanation in text

rounded, while the side in contact is plane (fig. 2, a-c). Where there are several parts combined, they are placed sometimes one behind the other, sometimes one beside the other (fig. 2, h). The diameter of the grains vary from 3 to 18 μ ; the average diameter is between 6.5 and 3 μ . The structure is slightly eccentric, depending on the arrangement by layers, which are not very evident except by examination with polarized light. The dark cross obtained by crossed Nicols is near the rounded end, and is seen especially in grains somewhat elongated (fig. 2, d and f). By a greater enlargement the nucleus of the layers can be observed (fig. 2, a). In the nearly globular grains the two dark striae cross in the middle (fig. 2, e). When the grains are submerged in water and under pressure of the cover glass, irregular cracks are seen,

which start often from the nucleus (fig. 2, *b* and *c*). The cause of these cracks is not the swelling but the pressure. In warm water the grains swell without cracks, and take the form of irregular linguiform corpuscles."

It is well known that the rhizomes of *Pteridium* have served on a large scale and still serve as food because of their richness in starch. In New Zealand and Australia they have been much used, and the natives of the Canary Islands make use of them also (C. BOLLE, Standorte der Farne auf den Canarischen Inseln, Zeitschrift für Allg. Erdkunde, Neue Folge xiv. 304). In 1884 I myself saw a peasant on the slope of Pic de Teneriffe dig up these rhizomes for this purpose. It is in the roasted and ground state that this root is used as food. According to HOOKER (Spec. Fil. ii. 199), Dr. B. CLARKE has written an article (Hook. Jour. Bot. 9:212) recommending the use of this food. But the extraction of starch as the Chinese of Ichang practice it seems to be very rare. I find, however, a citation of LABILLARDIÈRE which says: "Amylacea radicum substantia, quam eliciunt mandendo, silvicolae Cap. V. Diemen sustentantur" (AGARDH Recens. spec. gen. Pteridis 1839, p. 46).

BASEL, SWITZERLAND

TWO EPIPHYTIC ALGAE

JULIA W. SNOW

(WITH PLATE XVIII)

Pirulus gemmata, nov. gen.

This minute alga was first found in 1897 growing in a culture with other small algae in the botanical laboratory at the University of Basel, Switzerland. Though the exact source of the culture cannot be stated, it is known to have come from the vicinity of Basel. The alga was next found in a culture taken from some epiphytic mosses and liverworts from Guatemala presented to the writer by Miss F. G. SMITH in January 1909. Though search has often been made for it in different parts of the United States, it has never been observed, and any record of its occurrence in the country has escaped notice by the writer.

In its early vegetative state the alga shows nothing distinctive and might easily be taken for a small *Chlorella* or the germinating zoospore of some higher form (fig. 1), but in the shape of the adult cell and in its mode of reproduction it stands unique among all green algae.

In shape the mature cell is pyriform, either perfectly symmetrical or somewhat irregular, 0.0084–0.0112 mm. in length and 0.0056–0.007 mm. at its greatest breadth (figs. 2, 3). The color is a very light green. The parietal chloroplast is cup-shaped, with the large opening either at one side or at the smaller end of the cell, so that a portion of the cell is always colorless. A large vacuole is present (fig. 5a). No starch was found in either the material from Switzerland or in that from Guatemala. In the former no reaction for cellulose was obtained with the chloriodide of zinc, but in the latter a distinct reaction was shown with that reagent. A further difference between the two forms was noted in the number of nuclei. In the Swiss material the mature cells when stained with hematoxylin showed four distinct nuclei, and in some instances eight were counted; while in the material from Guatemala a cell

showed but a single nucleus (fig. 5*b*). In all other respects, however, in the shape and the size of the cells, the nature of the chloroplasts, and mode of reproduction, but slight variations in the two forms occurred. The different results obtained in the membrane tests might possibly be explained by a difference in the reagents used, in which case the only real difference would lie in the number of the nuclei. As this is an internal difference rather than an external one, the two algae have been regarded as forms of the same species.

The most distinctive characteristic of this alga is its reproduction. Whereas all other similar forms multiply either by fission or internal division, producing either zoospores or non-motile gonidia, this form reproduces by budding. The smaller end of the pear-shaped cell elongates, then a slight constriction occurs near the end, and a membrane is put across, forming a cell which is nearly spherical, with a diameter much smaller than the original cell (figs. 3, 4). This new cell does not become detached immediately, but again the smaller end of the parent cell elongates and a second cell is produced between the original cell and the one last formed. This is repeated continuously, and often a chain of 12-14 cells is produced before the cells separate, the oldest of the series being farthest away from the original cell (fig. 6). Growth usually begins in each new cell as soon as formed, so that there is a slight increase in size from the youngest to the oldest of the chain, and often the largest ones of these begin to reproduce themselves before the breaking up of the filament takes place (figs. 7, 8). Instances were observed where new cells were seen to originate from opposite ends of the parent cell, but this was a rare occurrence.

The alga was cultivated in pure cultures under various conditions and in various concentrations of Knop's solution, but was found to vary little except in rapidity of growth and length of filament or chain formed. The greatest increase in the amount of material occurred in 0.2-0.5 per cent Knop's solution and on agar-agar plus 0.2 per cent of the same solution; while the longest chains of cells occurred in the weaker concentrations, such as 0.05 and 0.1 per cent, and on agar with a 0.2 per cent solution. With an increase in concentration there was a regular decrease in the

length of the chain of cells formed, until in 1 per cent rarely more than two cells were found united and growth was very meager. If cultures were old, whatever the concentration of the solution there was almost a complete separation of the cells, except once in a 0.4 per cent Knop's solution, where the plant floated on the surface of the liquid, long chains of cells were found. Even in the longest chain, however, the connection between the cells seemed to be a frail one, the cells becoming dissociated so easily that it is a question whether the alga should be called a unicellular one or a filamentous one. In this respect it resembles closely *Stichococcus*, which is classified by CHODAT (1) as a filamentous form, but which probably should be regarded as a unicellular alga.

In what condition this alga existed in its natural surroundings it is impossible to say, since it could not be observed on account of its minute size; but when first noted in culture, the scattered chains consisted of but two or three cells, and indicated that when it was put in the culture it was in the unicellular form.

The direct cause of this fragmentation of the chains or filaments was not determined, but the process resembled so closely a similar fragmentation observed by KLEBS (3) in *Hormidium nitens* that the cause is probably the same. KLEBS observed in his cultures of *Hormidium* that the fragmentation took place either in an insufficient amount of nutritive salts, or in absence of sufficient moisture, and offers a hypothetical explanation of the phenomenon. His theory is that under these conditions the alga at first ceases to divide and then ceases to grow, but that nutrition may continue for some time. As a result, the cell becomes filled with organic nutritive material, whereby the walls become distended and the layer of cuticula binding the cells together becomes broken and the cells fall apart. LIVINGSTON (4), however, in his work on *Stigeoclonium*, believed that a fragmentation occurred as a result of osmosis, and found that the higher the osmotic strength of the nutritive solution the more readily the dissociation of the cells took place.

The phenomenon of filaments falling apart into individual cells each of which continues to live, and under favorable condi-

tions to grow out into a long filament again, is characteristic of most epiphytic filamentous algae, such as *Stichococcus*, *Hormidium*, *Stigeoclonium*, and the following form, and in all cases, whether there is a specialized mode of reproduction or not, this phenomenon must be most instrumental in disseminating the plant. If in the dry epiphytic condition the plant exists in the unicellular state, as would seem to be the case, the cells must be easily blown from one locality to another, and so bring about a wide dissemination of the species. But during a rainy season, undoubtedly those single cells produce filaments which again become broken up into individual cells when the dry conditions return.

There is but little doubt that the alternating wet and dry conditions of the environment in which they live are the means by which the polymorphic conditions of these aerial forms are brought about. As they change their form according to conditions, assuming the nature of either a filamentous or a unicellular alga, they must be regarded as transitional forms between the unicellular and the multicellular genera, and as such they form a most interesting group.

Pirulus, nov. gen.—Alga unicellular, or forming short, fragile, beaded filaments. Mature cell pear-shaped, color a light green: chloroplast cup-shaped, with large opening at one side or at the smaller end; no pyrenoid present. Reproduction by budding, in which the smaller end elongates and is cut off by a membrane, after which a separation may occur or not.

Pirulus gemmata, nov. sp.—Mature cell 0.0084–0.0112 mm. long and 0.0056–0.007 mm. at broadest portion. Membrane of cellulose; a large vacuole at the center and a nucleus present (4 or 8 nuclei in European form). Often forming fragile filaments of 12–15 cells.

Found on epiphytic liverworts and mosses from Guatemala, also in Switzerland.

Aeronema polymorpha, nov. gen.

Growing constantly on mosses and liverworts in certain places, and occasionally on the surface of flower pots in plant houses, is a microscopic polymorphic alga, which, according to conditions,

may assume the characteristics of a typical unicellular alga, or may take on the nature of a well defined branched filament.

An alga which undoubtedly belongs in this same genus was found first in Basel, Switzerland, and its life history traced under the guidance of Professor KLEBS (5), but the species here given has been found in various places in the United States and under different conditions, but principally in the vicinity of Northampton, Massachusetts. In which phase of its polymorphism this alga existed in its natural habitat cannot with certainty be stated; its size is so minute, that its identity can be determined only in culture, and there the form that it assumes depends entirely on the cultural conditions.

In its filamentous state it resembles most closely *Conferva* and *Bumilleria* in that each cell contains several chloroplasts which have a peculiar light and transparent color, without starch and pyrenoid (figs. 10-14). The profuse branching of this form, however, would prevent its being classified with either of these genera, which are strictly unbranched. In its unicellular condition (fig. 15) it is doubtful if one could distinguish it from a small *Botrydiopsis*. The cells are spherical, with a number of light-colored, parietal chloroplasts, but the fact that it may assume a filamentous state would probably place it far from this form in the generally accepted system of classification.

In the filamentous state so profuse are its branches that it often forms relatively large, more or less spherical complexes in which the branches radiate from a common center with apical growth. In a vigorously growing culture (as in 0.03 per cent Knop's solution) the filaments are cylindrical, and in each cell there are relatively few irregular parietal chloroplasts (figs. 11, 12). Only a single nucleus is present, which sometimes may be seen between the chloroplasts without staining.

It has been found that the concentration of the culture medium exerts a great influence on the form the plant assumes. In a series of cultures made in different concentrations of Knop's solution ranging from 0.05 per cent up to 1 per cent, it was found that from 0.05 to 0.3 per cent there was a regular increase in individuals, also in the length and number of filaments, which

varied from 0.0028 to 0.006 mm. in diameter; while from 0.3 to 1 per cent reproduction decreased, and the length and number of filaments diminished. This reduction in length was accompanied also by a great increase in the diameter of the cells and the assumption of a spherical shape, followed by an almost complete fragmentation of the filaments previously formed (fig. 15). The diameter of these cells reached as much as 0.0228–0.028 mm. In this condition a well defined reaction for cellulose was obtained in the membrane with the chloriodide of zinc, but this was not obtained in the filamentous stage. In some cases a strand of protoplasm was seen to extend from each chloroplast toward the center; this probably extended to the nucleus, though it could not be determined definitely.

The alga reproduces by means of zoospores 0.005–0.0065 mm. long and 0.0018–0.003 mm. broad (fig. 18). They are pointed at both ends, have a single chloroplast, a single cilium, and a pigment spot. They are very amoeboid in their motion, bending back and forth, and changing their shape from time to time. After a period of activity they come to rest, assume a spherical form, and germinate immediately. The zoospores are formed by the successive division of the contents of a mother cell into 2, then into 4, 8, 16, or many segments (fig. 17). Usually there are 16 or 32 from each cell. They may be formed from any cell, but they seem to be formed first in the central cells of a complex rather than in the ends of the filaments. They are liberated by the gelatinification of the whole membrane and its expansion by the motion of the zoospores until one by one the zoospores become liberated and swim away. Often the process is very slow.

In respect to the zoospores, as well as to the vegetative structure, the resemblance to *Conferva* and *Botrydiopsis* is manifested, as all three have amoeboid zoospores with a single cilium; a difference, however, lies in the fact that these zoospores have only one chloroplast, while the others have two.

The mode of germination of these zoospores and the development into filaments seem to be the same as occurs in the genus *Stigeoclonium*. Soon after a spore comes to rest (fig. 19), it divides into two, and then into a chain of four, the two outer

cells developing in opposite directions into filaments, while the two central cells protrude laterally and give rise to two more filaments (figs. 10-12). Any cell of any of these filaments seems capable of producing a branch, and by the continued growth and branching the large complexes are formed, radiating from the two original cells at the center. Early in their history, however, division occurs in these cells in all three directions of space, so that a parenchymatous mass is formed, from which the branches radiate (figs. 13, 14). CIENKOWSKI (2), in writing of *Stigeoclonium*, refers to a similar structure from which the branches radiate, and calls it a *sole*.

As the age of a culture increases, especially in cultures of high concentration, the tendency toward the formation of these parenchymatous masses increases until we find large solid structures with but little resemblance to a filamentous alga (fig. 16).

It has long been known that in the Conjugatae certain forms of desmids resemble closely a single cell of corresponding filamentous forms, as, for example, *Spirotaenia* and *Spirogyra*; *Cylindrocystis* and *Zygnema*; *Mesotaenium* and *Mougeotia*. A like similarity must be taken into account in the case of *Conferva* and *Botrydiopsis*, as the nature of the individual cells and the reproduction are almost identical. In this new genus it would seem that we have a transitional form between the well defined filament of *Conferva* on one side and the unicellular *Botrydiopsis* on the other. Or possibly *Conferva* might be an intermediate form between this and *Botrydiopsis*, as certainly the branched nature would indicate a higher development than the single filament. But the filament of *Conferva* is less fragile than the filament of this form, so it is difficult to say what would be the most correct classification.

LUTHER (5) and WEST (6) would place all algae characterized by the distinctive light green shade shown in this form into one class, the HETEROKONTAE, irrespective of their shape, size, filamentous or unicellular nature; but whether one accepts the views of these writers or retains the older classification, the genus *Aeronema* must be placed near to *Conferva* or *Bumilleria*.

Aeronema, nov. gen.—Microscopic branched filamentous alga, filaments according to conditions often becoming beaded and fragmented or forming more or less parenchymatous masses. Chloroplasts several or many in each cell; light in color, without pyrenoid. Reproduction by means of amoeboid zoospores with a single flagellum, a single chloroplast, and a pigment spot.

Found in Switzerland and the United States.

Aeronema polymorpha, nov. sp.—Diameter of filaments 0.0028–0.006 mm. No starch or oil present; membrane (in beaded filaments) of cellulose; 16 or more zoospores formed in a cell, each 0.005–0.0065 mm. long and 0.0018–0.003 mm. broad.

Found in Massachusetts.

The writer wishes here to express her thanks to Miss F. G. SMITH for material brought from Guatemala, and to Professor G. KLEBS for guidance and inspiration in the original study of these genera.

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3. KLEBS, G., Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen. Jena. 1896.
4. LIVINGSTON, B. E., On the nature of the stimulus which causes the change of form in polymorphic green algae. BOT. GAZETTE 30:289–317. pls. 17, 18. 1900.
5. LUTHER, A., Bihang till K. Sv. Vet.-Akad. Handl. 24:no. 13. 1899.
6. WEST, G. S., A treatise on the British freshwater algae. Cambridge. 1904.

EXPLANATION OF PLATE XVIII

All drawings except fig. 16 were made with a Zeiss 3 mm. objective and no. 6 ocular. Fig. 16 was made with a Zeiss 8 mm. objective and no. 6 ocular. An Abbé camera lucida was used in all drawings except in fig. 18, when two of the zoospores were drawn free hand.

Pirulus gemmata, nov. gen.

FIG. 1.—Young cells.

FIG. 2.—Mature cells.

FIG. 3.—Mature cells somewhat irregular because of crowding.

FIG. 4.—Different stages in the formation of filaments.

FIG. 5.—Optical section showing vacuole (*a*) and nucleus (*e*).

FIG. 6.—Mature filaments.

FIGS. 7, 8.—Filaments showing cells reproducing before dissociation.

Aeronema polymorpha, nov. gen.

FIGS. 9-12.—Young filaments.

FIGS. 13, 14.—Older individuals taken from a culture in 0.3 per cent Knop's solution.

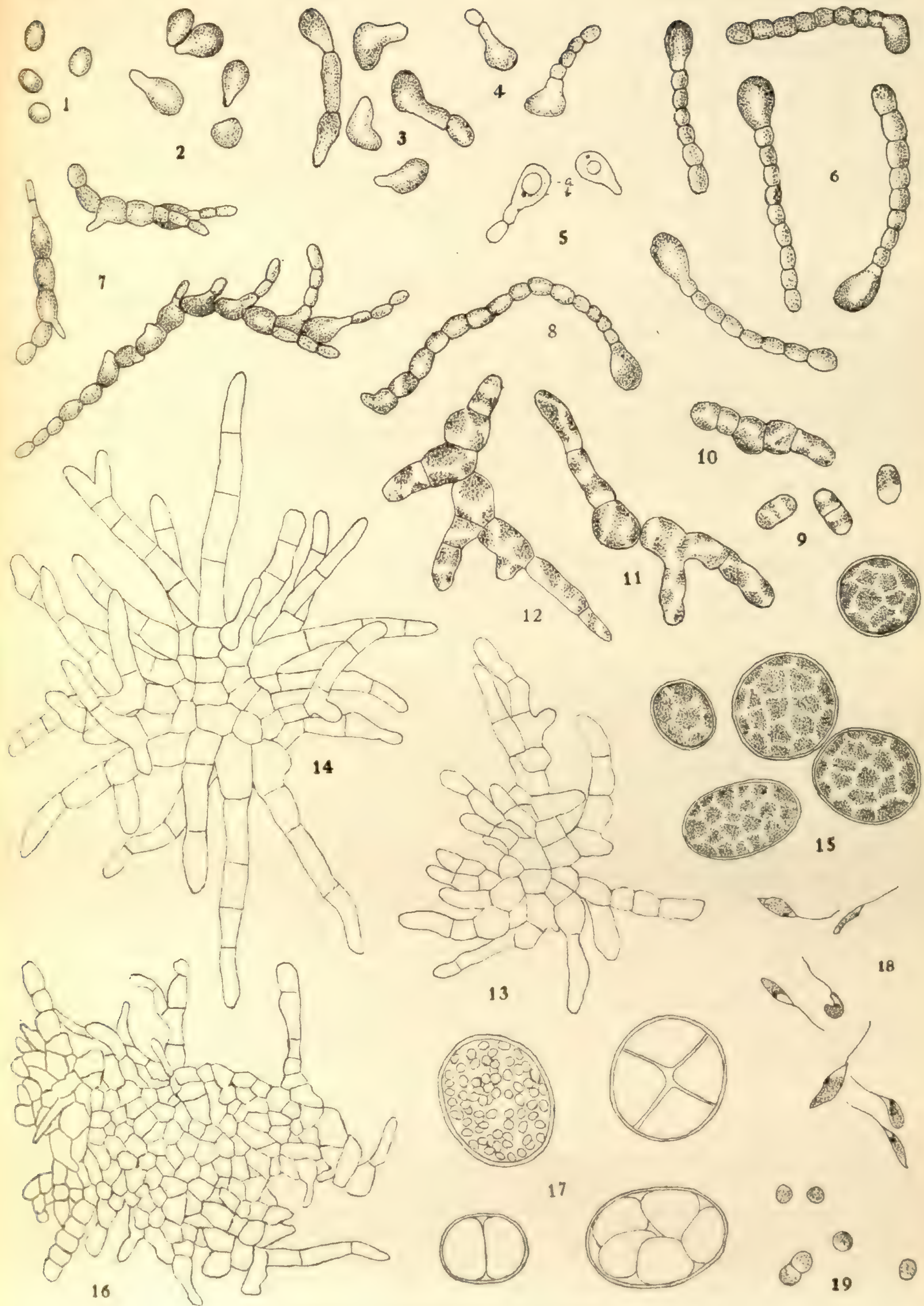
FIG. 15.—Unicellular condition taken from an old culture in 0.3 per cent Knop's solution.

FIG. 16.—Parenchymatous mass taken from an old culture in 0.05 per cent Knop's solution.

FIG. 17.—Different stages in the formation of zoospores from the unicellular condition.

FIG. 18.—Zoospores.

FIG. 19.—Germinating zoospores.



SNOW on EPIPHYTIC ALGAE

THE DEVELOPMENT OF THE SPORES IN PLEURAGE ZYGOSPORA

I. M. LEWIS

(WITH PLATE XIX)

Pleurage zygospora (Speg.) Kuntze, formerly reported from Italy alone, has been shown by the cultural methods employed by THAXTER and later by GRIFFITHS¹ to occur throughout this country. This species was first described by SPEGAZZINI² in 1878, and was placed in *Sordaria* as *S. zygospora*. It was later transferred from this genus by SACCARDO³ and placed in *Philocopra*. This transfer was made on the basis of the apparent number of spores being 16 in place of 8. Later (1898) KUNTZE⁴ described it as a *Pleurage*. This classification was retained by GRIFFITHS in his memoir. The species name *zygospora* has been retained throughout.

The position of this species depends upon the interpretation which is placed upon the mature ascospore. It is obvious that such an interpretation should be based upon a knowledge of the development of the spore. A cytological study of the peculiar appendaged condition of the spores in the genus *Pleurage* has not, so far as the writer is aware, been carefully made. A complete understanding of the nature of the primary appendages necessarily involves a study of the behavior of the nucleus of the primary sporogenous cell. This detail was not attempted by GRIFFITHS in his memoir on the Sordariaceae.

The spores of the species of this genus in which the primary appendage occurs are known to pass through a peculiar mode of development. The primary sporogenous cell is cut out of the cytoplasm of the ascus after the method described by HARPER.⁵ These

¹ GRIFFITHS, D. A., The North American Sordariaceae. Mem. Torr. Bot. Club 11:1-134. 1901.

² SPEGAZZINI, C., *Michelia* 1:227. 1878.

³ SACCARDO, P. A., *Sylloge Fungorum* 1:251. 1882.

⁴ KUNTZE, OTTO, *Revisio Generum Plantarum* 3:505. 1898.

⁵ HARPER, R. A., *Annals of Botany* 13:507. 1899.

cells are quite small, cylindrical, hyaline, straight or curved, and do not differ markedly in structure from the abundant epiplasm of the young ascus. They grow for a time and become transformed into filamentous cells, the length of which varies in different species. When one of these cells approximates its maximum length, the upper end begins to enlarge and forms an ellipsoid portion into which the greater part of the protoplasm migrates. This portion then becomes cut off by a cross-wall and forms the fertile cell of the spore. The remainder constitutes the so-called primary appendage. *Pleurance zygospora* shows upon a superficial examination that the spores are developed after this same general method.

Because of the peculiar interest attaching to this method of spore-formation, and also because of the great variability found to obtain in spores of *Pleurance zygospora* from collections made in the vicinity of Austin, Texas, the writer deemed it desirable to make a detailed cytological study of their complete development. The material for this study was grown in damp chambers on the natural substratum, and was prepared according to the methods employed in modern cytological technique. Flemming's solution, weaker formula, as a fixing agent left nothing to be desired. The best stain was found to be the Flemming triple stain. Sections 10 μ thick gave very good preparations for study.

The immature perithecia contain many different stages in the development of the ascus, so that the stages could be studied in unbroken continuity in any one section. The study of fixed and stained material was supplemented by the use of fresh material crushed in water on the slide, and then treated with dilute aqueous gentian violet or eosin glycerin.

The details of nuclear division in the ascus and the young spore were not studied critically, as it did not appear that the material was favorable for a determination of the phenomena of chromosome reduction. The primary nucleus of the young ascus is quite large, and the chromatin material appears to be divided into four parts, but spindle stages were not observed (figs. 1-3). The cytoplasm is quite vacuolate, and this condition increases with the rapid enlargement of the ascus (fig. 4). After the ascus reaches about one-half its mature size, the division of the primary nucleus

takes place, and this is followed quickly by two succeeding divisions, so that 8 cells are formed in the ascus in the usual way. These cells lie quite close together near the upper end of the ascus, are very small, and there is an abundant epiplasm (fig. 4). These are the primary sporogenous cells which later give rise to the fertile cells of the spores. They are cylindrical, hyaline, and the cytoplasm is more dense than the epiplasm surrounding them. The ascus has not at this time reached its mature size, and the spores appear as very minute cells in its upper end (fig. 4).

Further development from the primary cells was found to be quite variable in any one perithecium. In all cases, however, the sporogenous cell begins to elongate and to enlarge in all directions. It most frequently happens that the growth takes place faster on one side than on the other, so that the cell becomes somewhat crescentic in shape. It is also slightly bulged out near its middle (figs. 5, 6). It often happens that the nucleus of the young spore divides before the cell has grown to more than two or three times its original length (fig. 5), but this is by no means always the case. Frequently the nucleus remains undivided even after the cell has reached the length equal to half that of the ascus. In a few cases it was observed that the nucleus did not divide at all. As the cell elongates, its cytoplasm becomes vacuolate and more resembles the epiplasm from which it is derived. The nucleus usually divides, and after the daughter nuclei have moved apart, succeeding divisions take place until a number of free nuclei are present in the spore (figs. 6-10). The filamentous cell grows in length until in many cases it becomes longer than the ascus, and is consequently compelled to assume a spiral position. It is at this time almost uniform in diameter throughout its length, and the nuclei are distributed along the entire filament. The cytoplasm contains many vacuoles and the epiplasm is greatly reduced. The formation of cross-walls may or may not take place. Both types of asci occur in the same perithecium, but one type usually predominates in any one perithecium. In the cross-walled type the walls are usually formed at about the stage shown in fig. 6. Stages such as shown in figs. 10 and 11 never form cross-walls. In some perithecia there may be only a single ascus of the cross-walled type, while in others

this type predominates. In no instance has an ascus been observed in which both types occur. In all of the multicellular filaments, each cell has a nucleus, and the cytoplasm is apparently more dense than in the other type.

About the time the filament has reached its maximum length or slightly earlier, the two ends begin to enlarge, and the cytoplasm in these ellipsoid portions becomes very dense. Each end portion usually contains a single nucleus (fig. 10). No cases were observed in which two nuclei were present, but occasionally it appears that a nucleus does not migrate to the end of the filament, and in such cases the end portion becomes abortive. In the case of the multicellular type, the end portion which is enlarged may consist of a single cell or of two or more cells (figs. 8, 9). These enlarged end portions become the fertile cells of the spore, and at maturity are about $15-20 \times 25-40 \mu$ in size. The connecting filament is homologous in origin with the primary appendage of other species of the genus. This primary appendage is seen to connect the two fertile portions of a single spore in this species. Each of these fertile portions functions as a spore. The primary connecting filament persists for some time, but at the maturity of the perithecium and the shedding of the spores, it has almost disappeared, thus separating the two portions, and the ascus produces, therefore, the functional equivalent of 16 spores. The primary appendage in this species is either one multinucleate cell or a filament made up of a number of cells. In some cases the multicellular spores were observed to present a somewhat abortive appearance (fig. 8), in which case it happens that one fertile cell only is produced. Abortion is not uncommon in the other type of spore, so that often only five or six pairs of fertile cells are produced, or sometimes the number of fertile cells is different in the two ends of the ascus.

The question quite naturally arises as to the definition of a spore, and whether this species produces 8 or 16 spores. It was on this basis that SACCARDO transferred the species to *Philocopra*. Functionally 16 spores are produced, but morphologically there are only 8. These 8 spores are either three-celled, that is, two fertile cells connected by a long multinucleate cell (fig. 10), or they may be multicellular, consisting of two fertile parts connected by



a long multicellular sterile portion which eventually disappears. The basis of the structure and origin of the spores seems to me to be the proper basis for their definition. I regard this species, therefore, as eight-spored, and the classification of KUNTZE as the proper one.

The question concerning the probable significance of the two types of spores produced, while interesting, must remain more or less speculative. It seems probable that this condition must have been derived from ancestors which produced multicellular spores, and that the production of fertile and sterile cells is due to specialization and sterilization. The first step in this process might have consisted in the formation of the enlarged fertile cells, following which the connecting cells ceased to be functional. The loss of cross-walls and the consequent production of the unicellular appendaged type of spore, characteristic of this and other members of the Sordariaceae, could easily follow.

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EXPLANATION OF PLATE XIX

All figures were drawn from sections with the aid of a camera lucida, a Leitz $\frac{1}{2}$ oil immersion lens, and ocular no. 1, and are magnified 880 times.

FIGS. 1-3.—Young asci showing relatively large nuclei and rather dense cytoplasm.

FIG. 4.—Ascus about two-thirds mature size, with vacuolate epiplasm and 8 primary sporogenous cells.

FIG. 5.—Various stages in the growth of the spore filament.

FIG. 6.—Young spores showing the crescentic shape and with several nuclei; the ascus has not increased much in size.

FIG. 7.—Spore filaments of the cross-walled type; the spores are almost as long as the ascus, but the end portions have not begun to increase in size; this same appearance prevails in the other type of spores.

FIG. 8.—A later stage than fig. 7; some of the spores are abortive, a condition which frequently occurs.

FIG. 9.—Older stage of the same type of spore shown in fig. 8, with the ends becoming enlarged.

FIG. 10.—The unicellular type, showing the multinucleate condition and enlarged ends, each containing a single nucleus.

FIG. 11.—Mature spores of the type shown in fig. 10; secondary appendages derived from the epiplasm are shown.

FIG. 12.—Mature spore of the three-celled type.

NOTES ON GINKGO BILOBA¹

WALTER W. TUPPER

(WITH PLATE XX)

Among the gymnosperms, one of the groups most interesting from a morphological standpoint is the Ginkgoales, the only living representative of which is *Ginkgo biloba*, or maidenhair tree of China and Japan. This group is of special importance and value to the morphologist because of the close resemblance which its reproductive characters bear to those of the Archigymnospermae, and the many ways in which its vegetative anatomy resembles that of the lower conifers. Thus, the modern *Ginkgo biloba* forms the connecting link between the lower conifers and the Archigymnospermae. The presence of well-marked annual rings, and of opposite pits with bars of Sanio on the tracheids, and the absence of either terminal or diffuse xylem parenchyma in the branch of *Ginkgo* are some of its characters which show its close relationship with the pinelike or lower conifers.

During this last year, the writer has made some studies of the wood and short shoots of *Ginkgo*. Perhaps the most striking characteristic of the anatomy of the wood is the presence and distribution of crystal cells and wood parenchyma. SEWARD and GOWAN² say that in a fairly old root the medullary rays contain a few crystal sacs, and that the wood parenchyma also includes some crystal-containing cells. Nowhere in their paper do they refer to the peculiar arrangement of the xylem parenchyma, nor is it shown by any of their plates. In another part of this same paper they describe the occurrence of swollen parenchymatous cells, full of crystals, in the secondary bast, cortex, pith, and medullary ray tissues. Nothing peculiar, however, is noted regarding

¹ Contributions from the Phanerogamic Laboratories of Harvard University, no. 34.

² SEWARD, A. C., and GOWAN, MISS J., The maidenhair tree (*Ginkgo biloba* L.). *Annals of Botany* 14:135. 1900.

their distribution. PENHALLOW,³ GOPPERT,⁴ and others have described the existence of crystal cells, or idioblasts, in the branch of *Ginkgo*, and PENHALLOW has even added that they occur scattered throughout the wood and often in vertical series.

From a careful examination of the root, I have found that these idioblasts, or crystal-containing cells, and parenchyma cells invariably occur in longitudinal rows, or series, which run from ray to ray. In every single case these parenchyma and crystal cells were found in relation with a ray, as is shown in figs. 1, 2, and 3.

Fig. 1 is a radial section of the wood of the root, and shows the large, round, crystal cells, or idioblasts, in a longitudinal row connecting two rays. To the side of and intermingled with the crystal cells of this row are parenchyma cells, some of which appear as appendages of the rays. These parenchyma cells apparently give rise to the crystal cells, or else are modified into them. Some of the crystal cells are torn, due to the fact that the crystals of calcium oxalate which they contained were not fully dissolved by treating with hydrofluoric acid. The crystal cells are seen in contact with a ray in a tangential view in fig. 3.

The Ginkgoales are the connecting link between the Archi- and Metagymnospermae, possessing, as they do, motile sperm cells and other reproductive characters of the Archigymnospermae, together with anatomical characteristics of the Metagymnospermae, such as clearly marked annual rings, bars of Sanio, opposite pits on their tracheids, and only vestigial traces of centripetal wood (in their foliar organs). The wood parenchyma, however, is related to the rays, and extends in *radial* rows, unlike the *tangentially* distributed wood parenchyma found in the conifers. Wood parenchyma, like annual rings, appears to have been produced by woody plants as a reaction to the arrival of winter conditions in the geological and climatic evolution of the earth. Figs. 2 and 4, the former a radial, the latter a transverse section of the *Ginkgo* root, also show the peculiar distribution of the xylem parenchyma and crystal cells.

Like the Pineae, probably the oldest conifers, *Ginkgo* has its

³ PENHALLOW, D. P., A manual of the North American gymnosperms. p. 209. 1907.

⁴ GOPPERT, H. R., Monographie der Fossilen Coniferen. p. 266. 1850.

leaves borne on short shoots. One of the most noticeable things about the short shoots of *Ginkgo* is the fact that quite frequently they branch within the wood of the limb out of which they grow. In fig. 5 we have a transverse section of a branching short shoot, showing the two divisions entirely separate from each other, yet still within the wood of the branch. Fig. 6 shows this same branching short shoot sectioned nearer the pith, with the short shoot not yet divided.

SEWARD and GOWAN (*l.c.* p. 132) say that in some instances the short shoot of *Ginkgo* may branch like the trunks of *Cycas*. To illustrate this they have reproduced a natural-sized cut (*l.c.* pl. 9, fig. 42) of a branching short shoot. The branching to which they refer, however, takes place entirely outside of the wood of the limb, as is shown by their figures.

It is of special interest in this connection to note that a new araucarian conifer, *Woodworthia*, from the Triassic of the Fossil Forest of Arizona, which has been examined and described by Professor JEFFREY⁵ has short shoots which likewise divide within the wood of the branch. This gives us convincing evidence that the araucarian conifers are an old group, and have possibly come from the same stock as the Ginkgoales. Unlike the short shoots of *Ginkgo*, those of the araucarian conifer mentioned apparently never grew out into long shoots.

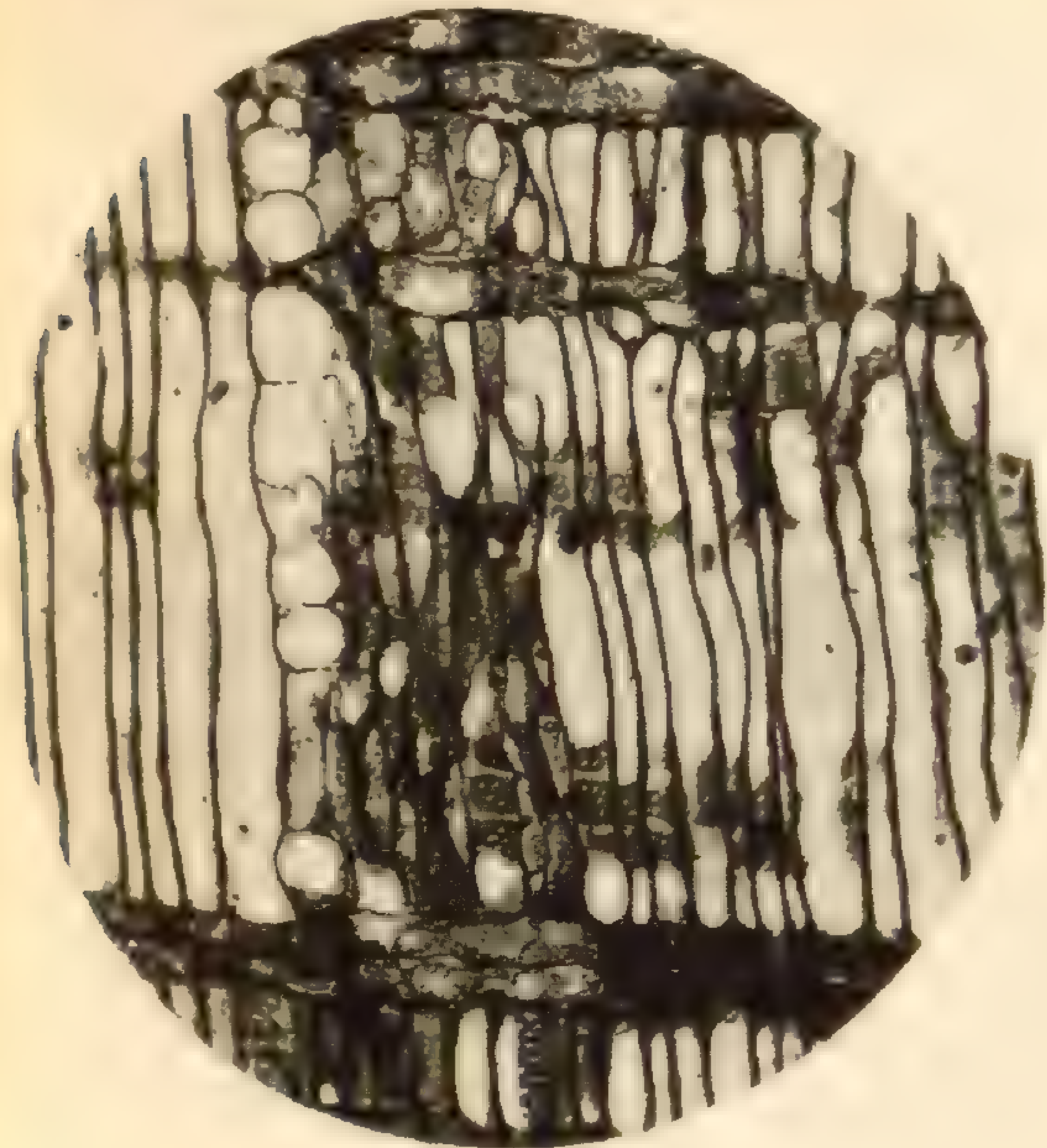
Like the Ginkgoales and araucarian conifers, the older Abietineae likewise had short shoots. It would be interesting, were the material available, to examine the short shoots and woody branches of *Prepinus*, the probable ancestor of the Abietineae, in search for branching within the wood of the limb.

Summary

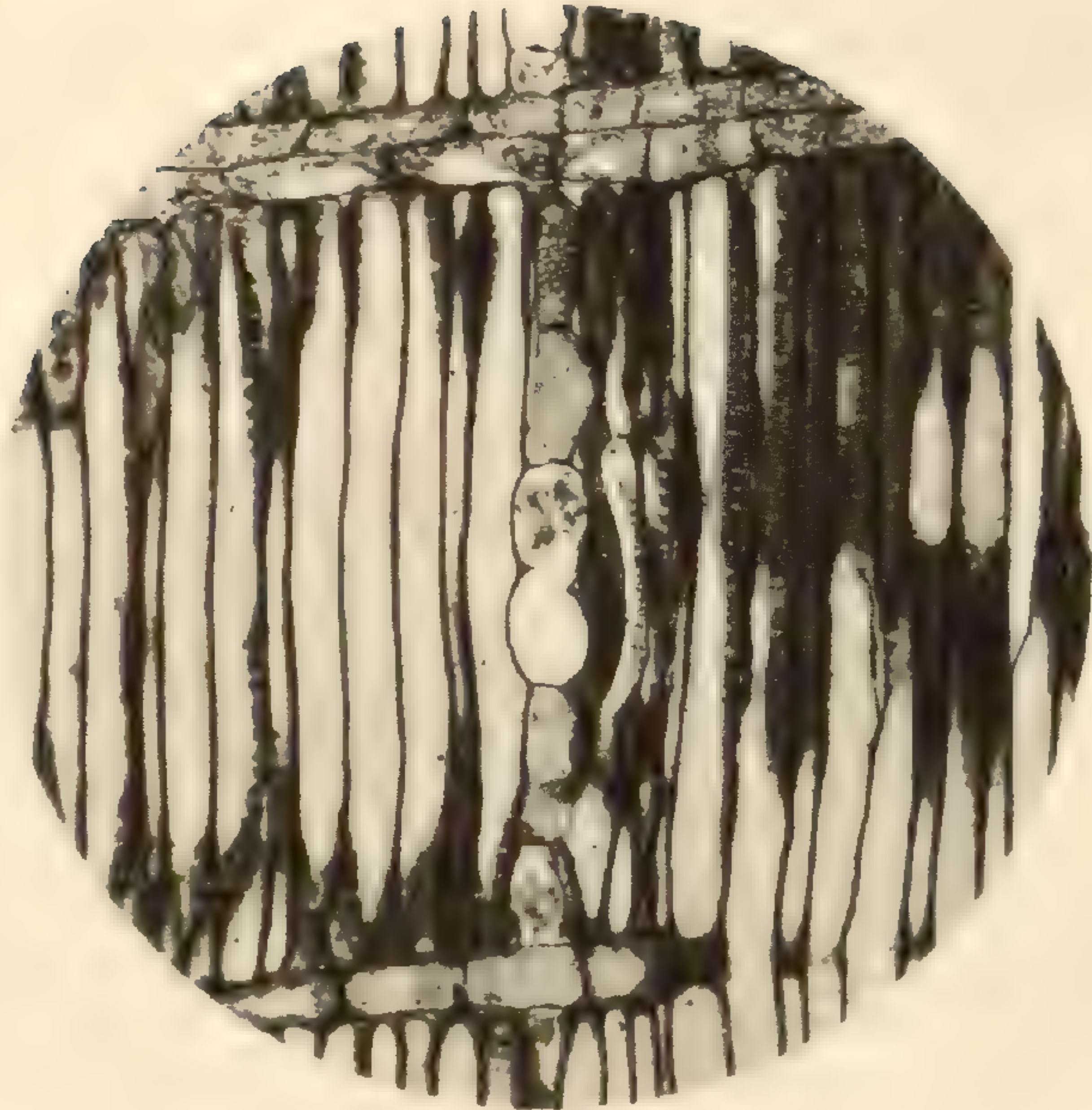
The root of *Ginkgo biloba* contains crystal cells and wood parenchyma distributed in rows or series which run longitudinally throughout the root in radial planes.

All of these rows of cells are in contact with at least one ray. In some places the wood parenchyma cells can be distinguished

⁵ JEFFREY, E. C., Proc. Boston Soc. Nat. Hist. 34: pls. 31, 32. 1910.



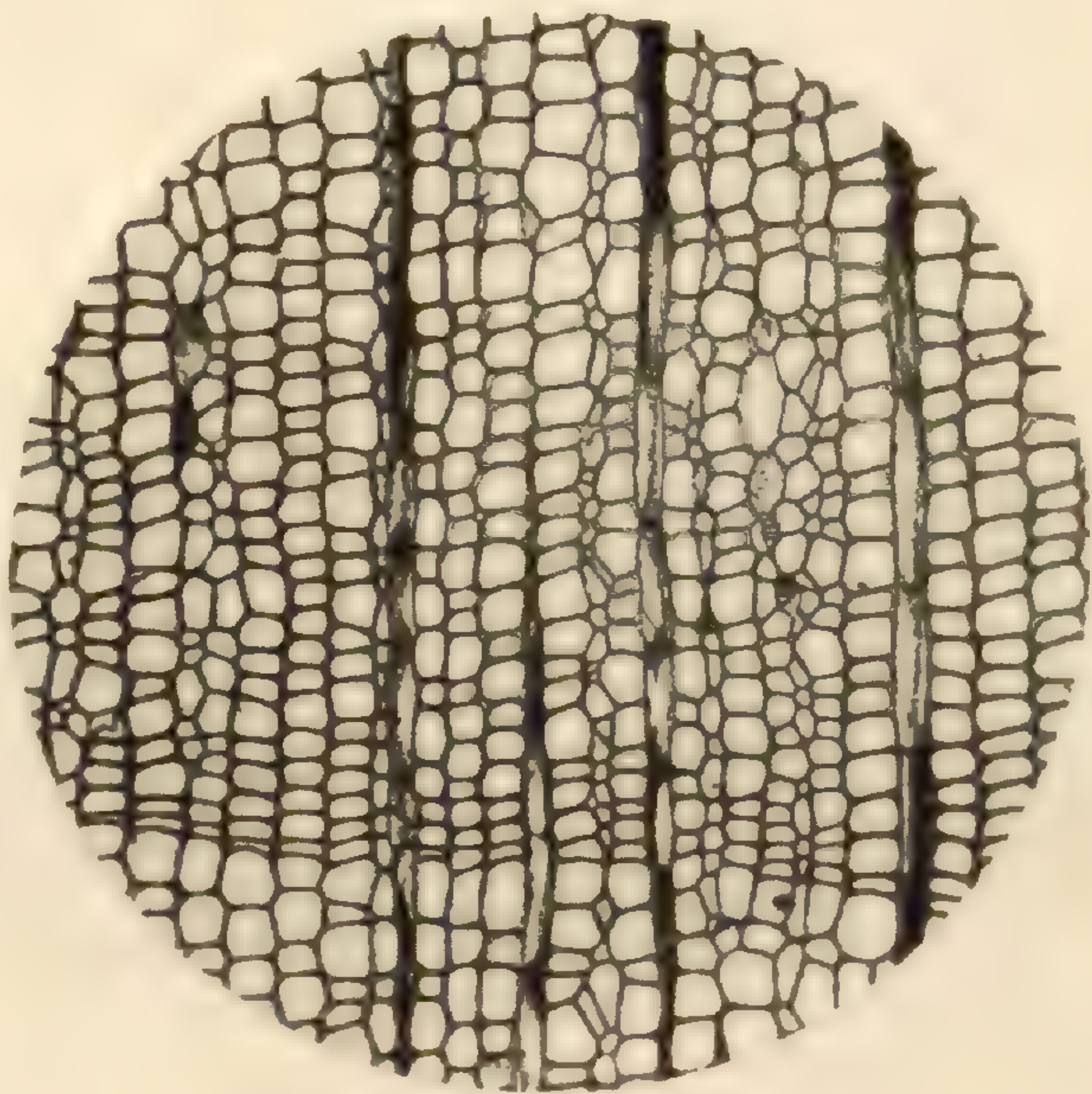
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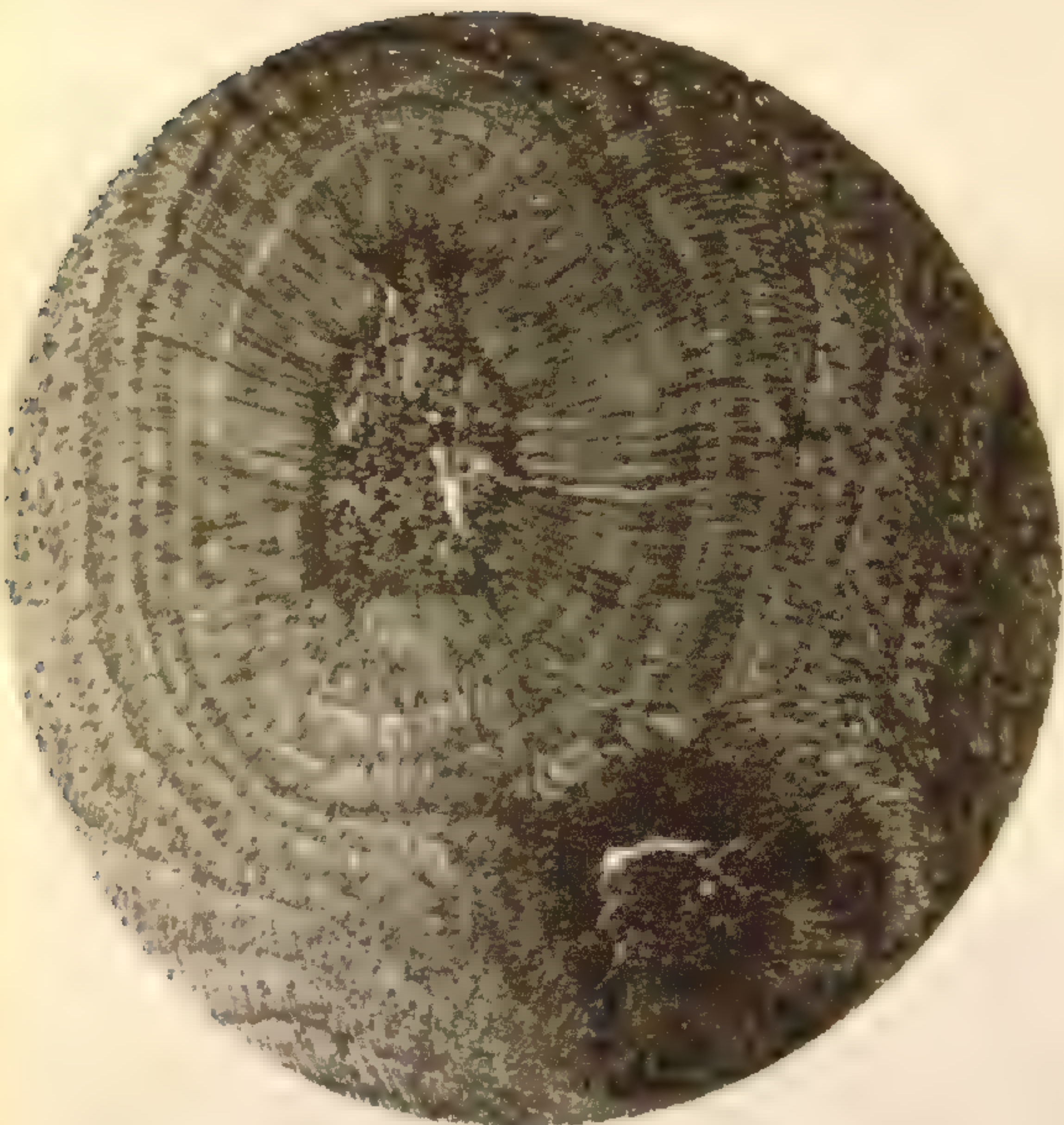
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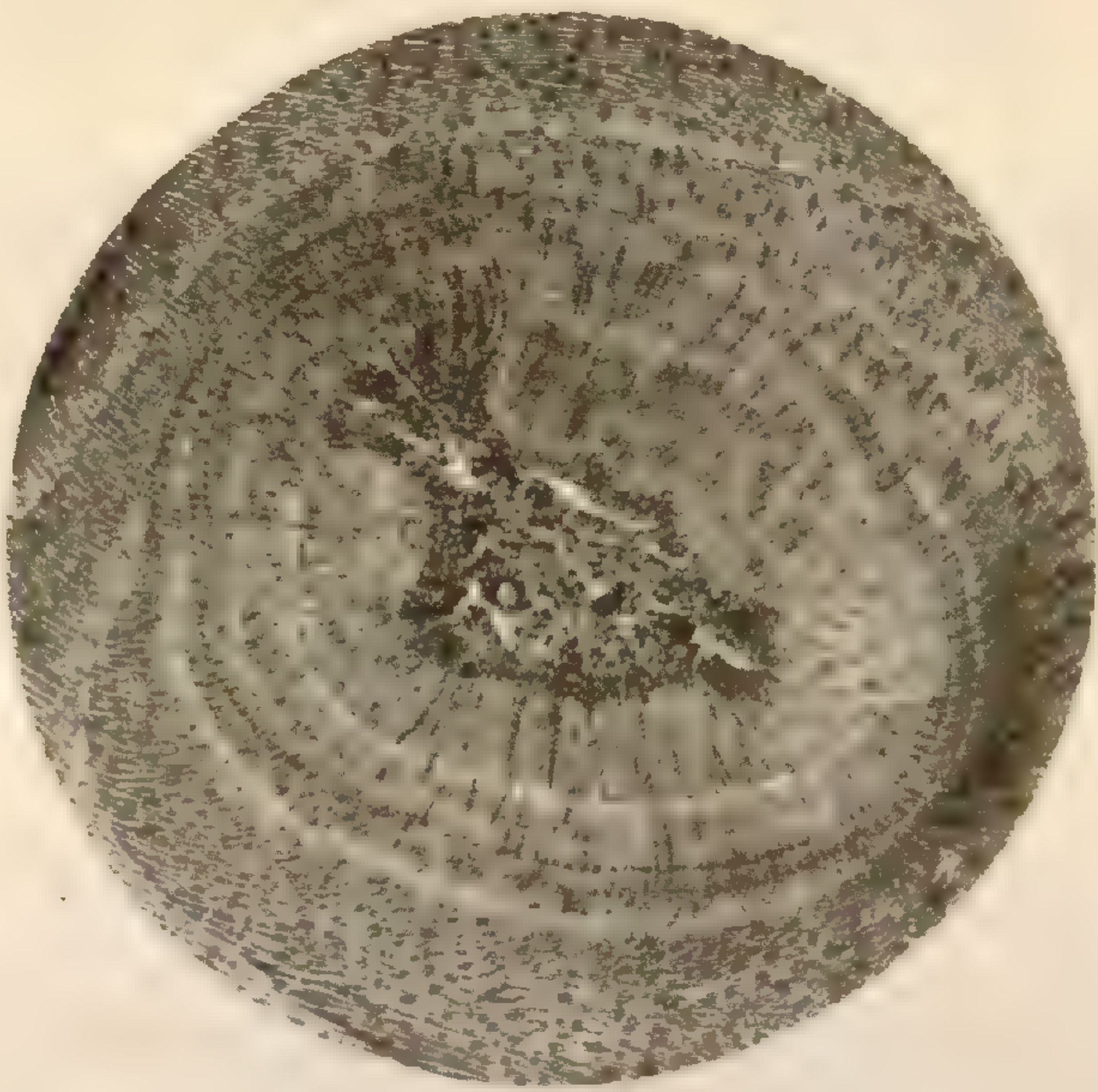
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4



5



6

TUPPER on GINKGO

as appendages of the rays. The crystal-containing cells seem to be a modification of the parenchyma cells.

The fact that all of the xylem parenchyma found in *Ginkgo* is very differently distributed from that found in the conifers (radial and not tangential) suggests that it is a primitive type.

The short shoots of *Ginkgo* frequently divide within the wood of the branch. The only one of the conifers which is known to have such a peculiarity is the new araucarian genus *Woodworthia*.

This work has been done in the Phanerogamic Laboratories of Harvard University. The writer is indebted to Professor JEFFREY for advice and guidance throughout the investigation, and for aid in securing the accompanying photomicrographs.

HARVARD UNIVERSITY

EXPLANATION OF PLATE XX

Ginkgo biloba

FIG. 1.—Radial section of root, showing crystal-containing cells in contact with a ray, and distributed in a row (intermingled with parenchyma cells) which runs longitudinally along the root; parenchyma growing out from rays; $\times 80$.

FIG. 2.—Radial section of root, showing two rays connected by a row of crystal cells; $\times 80$.

FIG. 3.—Tangential section of root; $\times 80$.

FIG. 4.—Transverse section of root; $\times 80$.

FIG. 5.—Transverse section of branching short shoot, showing the divisions entirely separate from each other, yet still within the wood of the branch; $\times 12$.

FIG. 6.—Transverse section of branching short shoot seen in fig. 5, sectioned nearer in toward the pith of the branch, showing the short shoot undivided; $\times 12$.

THE ORIGIN OF THE CHLOROPLASTS IN THE COTYLEDONS OF *HELIANTHUS ANNUUS*

EDWIN C. MILLER

(WITH PLATE XXI)

There are two prevalent opinions in regard to the origin of chloroplasts in seedlings. One group of investigators holds the view that the chloroplasts originate directly from the cytoplasm of the cell. According to them, the mature seed from which the seedling originates contains no chloroplasts. They hold that if any chloroplasts are present in the young embryo, they lose their color and disintegrate at the ripening of the seed, and that at germination the protoplasm in the cells of the cotyledons gives rise to new chloroplasts which function during the period of activity of these organs. The other group of investigators maintains that the protoplasm of the cell never gives rise to chloroplasts, but that the fertilized egg contains chromatophores which have been derived directly from the parent plant. During the development of the egg into the embryo these chromatophores multiply, and in this manner provide every cell of the embryo with chromatophores. In many seeds before maturity the chromatophores have become differentiated into chloroplasts, which are plainly visible. During the ripening of these seeds their chloroplasts lose their color and shrivel up, and on this account they are difficult to detect in the mature seed. At germination, however, the chloroplasts again become active and assume their original form and color.

SACHS (1) states that the chloroplasts arise in the young cells by the separation of the protoplasm into portions which remain colorless and others which become green and sharply defined. He holds that the process can take place by very small particles, originally of a different nature from the apparently homogeneous protoplasm in which they are distributed, collecting at definite places and appearing as separate masses.

MIKOSCH (2), after an examination of the seeds and seedlings of *Helianthus annuus*, reached the conclusion that there are no chromatophores present in the resting seeds of this plant, but that during germination the chloroplasts arise directly from the protoplasm of the cells. He holds that their origin is due to the condensation of the cell plasma in definite places. This condensation he thinks is probably brought about by a loss of water in those parts. The condensed parts soon take on the green color and become the chloroplasts. This process of formation goes on independently of light. The bodies thus formed are at first rod or spindle-shaped, but later assume the typical disk shape of the chloroplasts.

BELZUNG (3), after a lengthy investigation of the ripening seeds as well as of the mature seeds and seedlings of many plants, came to the following conclusions: (1) that the free growth of starch grains can take place without the intervention of leucoplasts; (2) that the chloroplasts are formed directly by a differentiation of the protoplasm; (3) that the chloroplasts can also be formed at the expense of the starch grains which have their origin in the cytoplasm of the cell. The severe criticism of his work by SCHIMPER (4) led BELZUNG to traverse anew his previous work, and in a paper published in 1891 (5) he verified his previous conclusions. In this investigation he used as material *Phaseolus vulgaris*, *Lupinus albus*, *Lupinus elegans*, *Faba vulgaris*, *Pisum sativum*, and other plants. According to his observations, the young embryo contains no chloroplasts. The starch grains formed in the young embryo are laid down in the vacuoles of the protoplasm. He holds that those who claim that starch grains are the product of leucoplasts are in error, and that the leucoplasts defined by different investigators are simply the boundaries of the vacuoles in the protoplasm. The green color of the embryo in many plants is due to a green pigment distributed throughout the protoplasm of the cell. According to BELZUNG, therefore, there are no chromatophores present in the embryo, and consequently none in the mature seeds. At germination the simple starch grains of the seed disintegrate, and numerous compound grains of transitory starch appear in various parts of the protoplasm. These com-

pound grains are formed as follows. Each large vacuole is composed of two to five secondary ones. In each of the latter a small starch grain is formed, the several grains making the compound grain. As this grain disappears, an infiltration of the green pigment takes place and thus a chloroplast is formed. BELZUNG made most of his observations upon fresh material and used iodine green for his staining.

MEYER (6), after his thorough investigation of the structure and nature of the chloroplasts, reached the conclusion that the origin of the chromatophores does not take place in the young plant cells, but that they are derived from other cells in which they previously existed, and that they increase in number by the division of those already present.

SCHIMPER (7) found chromatophores present in the embryo sac and egg of numerous phanerogams. Although his observations were rather meager, he concluded that the chloroplasts thus present in the young embryo were not reabsorbed in the ripening seed, but that they merely become colorless and lose their function. Upon germination, after they have again taken on the green color, they become functional.

BREDOW (8) examined a large number of green, yellowish, and colorless seeds, and came to the conclusion that chloroplasts were present in all of them, although they stain very poorly and are hard to detect. He studied the seeds of *Pisum sativum*, *Robinia Pseudacacia*, *Cucurbita Pepo*, *Acer crataegifolium*, *Ipomoea splendens*, *Pinus austriaca*, and *Lupinus luteus*, both in the fresh condition and after the treatment with reagents. The sections of the fresh seeds were mounted in cell sap or in weak glycerin. Good results in staining the chloroplasts were obtained by treating the sections for several days with a concentrated solution of picric acid. This colored all the proteid material yellow, but the chloroplasts showed a deeper stain than the other cell contents. In sections treated with picric acid, washed with water, and then stained with hematoxylin, the chloroplasts also showed well. BREDOW found that the chloroplasts of the seed increased during germination by simple fission, and also by a division of one chloroplast into as many as ten or twelve smaller ones by numerous irregular

divisions. He believed that the greening of these numerous small bodies led the earlier investigators to the conclusion that the chloroplast originates directly from the protoplasm of the cells of the seedling. It is worthy of note that BREDOW worked with *Lupinus luteus*, a seed in which BELZUNG found no chloroplasts at all.

FAMINTZIN (9) investigated the origin of chloroplasts in seedlings, and especially the manner in which the chloroplasts, if present in the seed, divide. He selected as his material for investigation the seeds and seedlings of the sunflower, using the fresh material of seeds and of 16 and 24-hour seedlings. By ZIMMERMAN'S method he was unable to distinguish the small aleurone grains and particles of proteid from the chloroplasts, since the whole cell content stained red. He then originated a modification of this method by treating the sections previous to fixing and staining with acetic acid. The sections were left in 1 per cent acetic acid for 24 hours, or less for a stronger solution of the acid, and were then fixed and stained according to the method of ZIMMERMAN. By this means the protein granules and grains remained colorless or were only faintly colored red, while the chloroplasts and other protoplasmic structures were stained a deep red. In this way FAMINTZIN was able to make out the chloroplasts in the resting seed and during the early stages of the germination. Some of the chloroplasts in the resting seed are in the cytoplasm lining the cell wall, but by far the greater part of them, according to him, are in the film of protoplasm which surrounds the protein grains. Upon placing fresh sections of the material in the light, he observed that these small bodies on the protein grains took on a yellowish or brownish color. By identifying these bodies in the young stages of the seedlings, FAMINTZIN concluded that the seeds of the sunflower contain chloroplasts, and that these by simple fission give rise to those of the seedling.

The seeds for the following investigation were planted in white quartz sand and placed in the greenhouse at a temperature of 65-75° F. At intervals of 12 hours the seedlings were taken up, and parts of the cotyledons near the middle were placed in the fixing material. This was carried on until the plants were above

the ground and had become true photosynthetic structures. The seedlings were examined at 11 different stages exclusive of the seed. Chromacetic acid solution was used for fixing, and the material was washed, dehydrated, and imbedded in paraffin in the usual manner. Various methods of staining were tried. By the use of ZIMMERMAN'S method the same difficulties were encountered as were experienced by FAMINTZIN. In the later stages of the seedlings the chloroplasts are plainly differentiated, but during the early stages they could not be distinguished at all from the protein granules in the cell. Sections which had been treated with picric acid and then tinged with eosin also showed the chloroplasts plainly in the later stages of the seedling, but during the earlier stages the protein matter, as well as the chloroplasts, takes a deep stain and the identity of the latter is uncertain. Sections were then treated according to FAMINTZIN'S modification of ZIMMERMAN'S method. One series of sections was placed in 30 per cent acetic acid for 30 minutes, then washed with running water and transferred to 0.2 per cent acid fuchsin. After being allowed to stand for 24 hours in this solution, the sections were washed in running water for 12 hours, dehydrated in 95 per cent and absolute alcohol, cleared in xylol, and mounted in balsam. Another series of sections was treated in the same manner, except that they were left in the 30 per cent acetic acid 45 minutes. The results obtained from the last series were the most satisfactory, and the examination of the material was made upon these sections.

The sections first examined were those of seedlings which were fully developed, and the number and position of the chloroplasts in the cell were clearly evident (fig. 12). Those next examined were of seedlings 12 hours younger, and fig. 11 shows the usual position of the chloroplasts at this stage. This method was continued step by step back to the original seed, since obviously the best means to find the nature of the origin of the chloroplasts is to trace them backward in this manner from stages in which there can be no doubt at all as to their position and identity. The chloroplasts, as shown clearly in figs. 1-12, occupy the normal position in the cytoplasm of the cell at all stages of the development of the seedling. In the resting seed, according to our opinion,

they are present in their usual place but are very minute. As the seed begins to germinate, they increase in size and then begin to divide by simple fission. The chloroplasts of the seed are thus the bodies which give rise to the chloroplasts of the mature seedling. The numerous small round bodies which are on the surface of the protein grains, and which take the red stain after the same manner as the chloroplasts, we do not consider as chloroplasts, since in the first place they are entirely too numerous to correspond with the number of chloroplasts in cells where their identity cannot be doubted, while the number of chloroplasts found in their normal position closely corresponds to the number which is found in the later stages of development. Also, these small bodies are plainly evident upon the protein granules in advanced stages of germination, when there is not the least doubt as to the identity of the chloroplasts. We agree with FAMINTZIN that the chloroplasts are present in the resting seeds of *Helianthus annuus*, and that they alone give rise to those of the seedling. We think, however, that he is in error in considering the small bodies which cover the protein granules as chloroplasts. What these bodies are we are unable to tell, but it seems evident that the stained bodies observed in the natural position of the chloroplasts account for all which appear in the seedling.

In conclusion I desire to extend my sincere thanks to Professor A. W. EVANS, at whose suggestion the work was undertaken, for his able advice and criticism; also to Dr. GEORGE E. NICHOLS, who gave me valuable advice in the preparation of material.

YALE UNIVERSITY

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EXPLANATION OF PLATE XXI

The abbreviations used are as follows: *c*, chloroplast; *t*, protoplasm; *p*, protein grains; *pf*, protein grain with bodies designated as chloroplasts by FAMINTZIN; *dp*, protein grains beginning to disintegrate; *n*, nucleus; *pt*, protoplasm and disintegrated protein grains; *v*, vacuole.

FIG. 1.—A lower palisade cell from a cotyledon of the resting seed; the protein reserve is seen in the form of large grains (*p*); the chloroplasts are seen in their usual position near to the cell wall; seven chloroplasts are visible in this section; $\times 600$.

FIG. 2.—A palisade cell from the cotyledon of a seed 12 hours after planting; the protein grains are still intact; the protoplasm has become vacuolated and active; at either end of the section of the cell the chloroplasts are seen; $\times 600$.

FIG. 3.—A palisade cell from the cotyledon of a seed 24 hours after planting; the protoplasm has become dense and shows no definite structure; the chloroplasts are still small; $\times 600$.

FIG. 4.—A cell from the palisade layer of the cotyledon of the seed 36 hours after planting; the chloroplasts (*c*) have increased in size; the rudimentary hypocotyl and root of the seed have not yet penetrated the seed coats; $\times 600$.

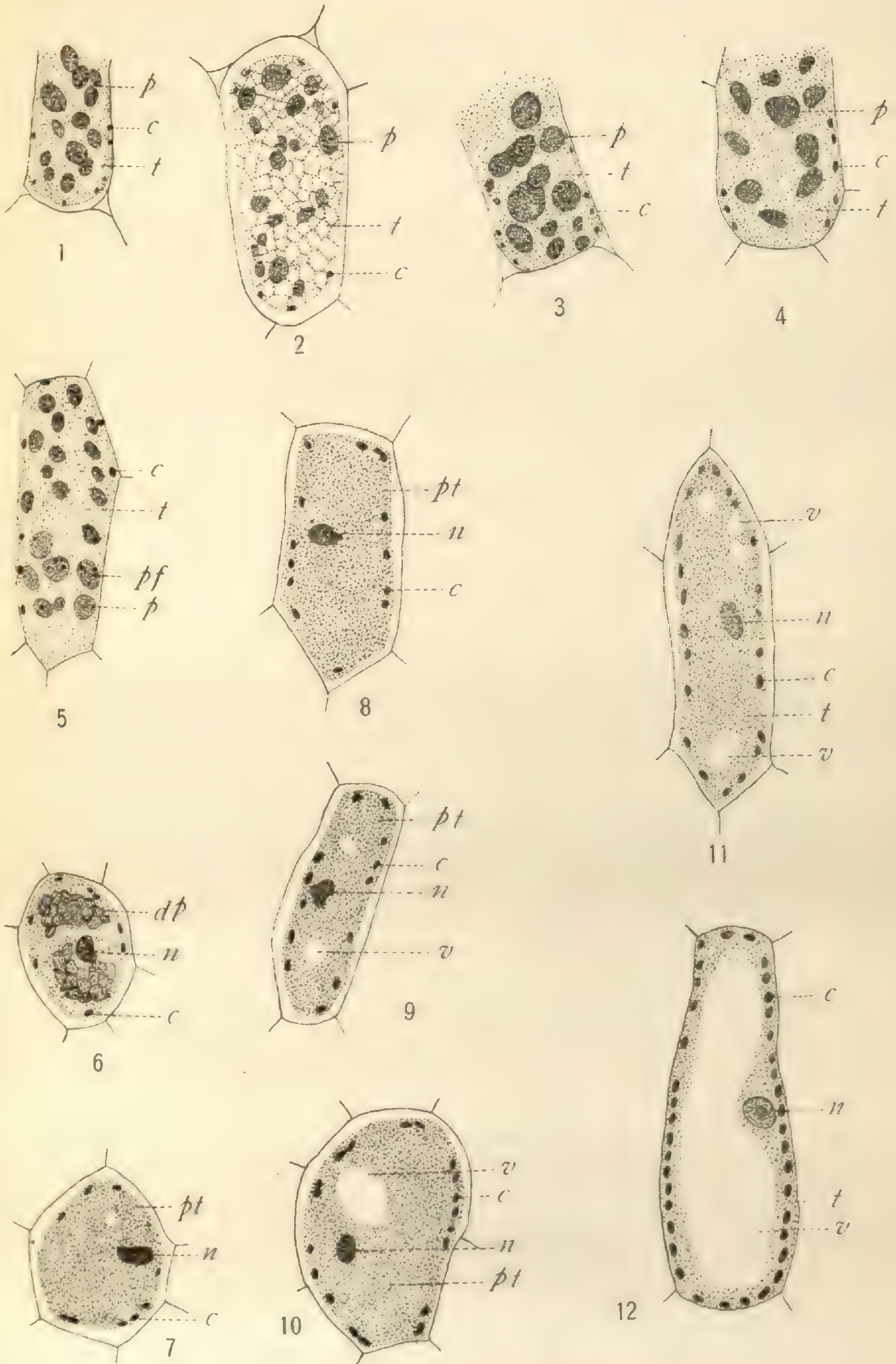
FIG. 5.—A palisade cell 48 hours after the planting of the seed; on the protein granules (*pf*) may be seen the bodies designated by FAMINTZIN as chloroplasts; the hypocotyls in the seedlings have a length of 0.6 cm.; $\times 600$.

FIG. 6.—A cell from the spongy layer of a cotyledon in a 60-hour seedling; the protein granules (*dp*) are plainly disintegrating; with the stain used, the nucleus first shows at this stage; $\times 600$.

FIG. 7.—A cell from the spongy layer of a cotyledon of a 72-hour seedling; the hypocotyls of the seedlings have reached a length of 2.5-3.5 cm.; the protein grains have now disintegrated and the cell content has become very dense; the chloroplasts are beginning to increase by division; $\times 600$.

FIGS. 8-11.—Cells from 84, 96, 108, and 120-hour seedlings; the increase in size and number of the chloroplasts at different stages can be plainly seen; during each succeeding stage the cell content becomes less dense and vacuoles appear; $\times 600$.

FIG. 12.—A palisade cell from a cotyledon of a 140-hour seedling; the seedling has become independent and the cotyledon is a typical foliage organ; $\times 600$.



BRIEFER ARTICLES

TWO SPROUTING CONIFERS OF THE SOUTHWEST

(WITH FOUR FIGURES)

The ability of conifers to produce coppice growth is limited to a few species, and most if not all of them occur in the United States. The coppicing of *Sequoia* has for a long time been a classic example, while sprout reproduction of the pitch pine (*Pinus rigida* Mill.) of the east and shortleaf pine (*Pinus echinata* Mill.) in the south is of considerable importance. During the past year extensive monogenetic reproduction of alligator juniper (*Juniperus pachyphloea* Torr.) and Chihuahua pine (*Pinus chihuahuana* Engelm.) was noted in the Garces National Forest along the international boundary between Mexico and the United States. This was very common for the region and was found in practically every stand where either of the species occurred.

The two most prominent stands of Chihuahua pine showing coppice origin were found in Boss Canyon in the Atascoso Mountains and to the south of the historic Mowry Mine in the Patagonia Mountains. The stand that occurs in Boss Canyon is especially prominent, since it extends the range for the species west of the Santa Cruz River and occurs at the remarkably low altitude of 1300 meters. Although an outlying body, it shows an optimum development for the species in the United States. According to a rough estimate, there are 500-600 Chihuahua pines over 15 cm. in diameter breast-high, with a reproduction that seems slightly inadequate to maintain the present stand. Fully two-thirds to three-fourths of the large seedlings and small saplings show severe injury by cattle, which usually consists of a broken leader and side branches (fig. 1). It is only rare seedlings in the most inaccessible areas that do not show this injury, and if it were not for the ability to sprout, reproduction would soon be missing. Typical sprouting over this area is confined to trees under 5 cm. in diameter, which send up most of the shoots from the root collar or the first 30 cm. above ground, although a large number of the saplings show groups of well formed buds at the nodes of both the leader and the branches. These buds occur for the most part on trees below 20 cm. in diameter at breast-height, and are usually confined to the lower half of the trunk and the lower portion of branches.

Near the Mowry Mine in the Patagonia Mountains there occurs a stand of Chihuahua pine which represents an excellent distribution of all sizes of trees up to 30 cm. in diameter and 9-15 meters tall. Many trees from 7.5 cm. up have been cut for mine timbers, and there is some



FIGS. 1, 2.—Fig. 1, Sprouts on Chihuahua pine as a result of injury by cattle; collected in Boss Canyon; fig. 2, Sprouts on Chihuahua pine as a result of forest fires; collected in Flux Canyon.

grazing injury. Not a single case was found where the stumps of trees smaller than 7.5 cm. in diameter had failed to produce thrifty sprouts, and fully 30-50 per cent of the stumps of trees up to 22.5 cm. in diameter had produced very thrifty sprouts, most of the fail stumps occurring

between the 15 and 22.5 cm. classes. It was only rarely that stumps over 22.5 cm. had produced any sprouts, while many stumps of 30 cm. and larger showed an entire lack of sprouting ability in older trees.

Recuperation after fire was well shown in Flux Canyon, which lies to the north of the Mowry Mine. A few scattering veterans had produced a fair amount of reproduction, which was mostly in the seedling stage. A severe ground fire which killed back several Emory oaks (*Quercus Emoryi* Torr.) and whiteleaf oaks (*Quercus hypoleuca* Engelm.) also killed back most of the Chihuahua pine reproduction. In every case where the dead leader of the pine remained, and in many cases where it was missing, 3-20 vigorous sprouts developed (fig. 2). It should not be inferred that this reproduction is more fire resistant than that of the oaks, for no information was available as to the amount and distribution of litter.

In the three stands already mentioned, as well as in various other places in the Patagonia Mountains, Canelo Hills, and Huachuca Mountains, a remarkable feature of the sprout growth was the early age at which cones were produced. A single case was found in Lyle Canyon where a tree 15 cm. in diameter breast-high and 7.5 meters tall was producing a green cone on an adventitious shoot only 30 cm. long which occurred 1.2 meters above ground. A few cases were found in which sprouts 7-10 years old were producing 1-3 cones each, and it was quite common to find sprouts 10-20 years old bearing 3-30 cones.

No study was made as to the relative rate of growth of sprouts and seedlings. Naturally the slow growth of the distinctly seedling period is not found in the sprout growth, but it is not known if the height growth of the sprouts culminates before the seedlings, as is the case with broad-leaved trees. No difference in form was noticed, although careful measurements might show a difference in form factor.

Even more remarkable is the sprouting of alligator juniper. In the northern portion of its range this species normally shows a large percentage of the trees with one or two shoots at the bases of the trees. These weak shoots are rarely over 15 cm. tall, and simply maintain life or die down, and are occasionally replaced by other equally weak shoots. In extensive trips over the Lincoln National Forest, where these small sprouts are common, not a single cut-over area showed any reproduction from the bases of the trees. There is a single tree between Capitan and Bonito, however, which was pollarded, and in May 1907 had 139 sprouts varying from 5 to 45 cm. in length (fig. 3). The same sort of sprouts were noted at the bases of trees in the Gila National Forest, but in the

vicinity of Glead, Arizona, where rare specimens of the species occur, no sprouts were found.

Along the Mexican boundary this species is usually a minor one, but it probably reaches here the maximum individual development that occurs in the United States. For the most part, it is found in valleys and canyons and on terraces and slopes, closely associated with the evergreen oaks and usually extending somewhat beyond the upper limit



FIG. 3.—Root collar sprouts and pollard sprouts on alligator juniper as a result of cutting; Lincoln National Forest, N.Mex.

of Arizona white oak (*Quercus arizonica* Sarg.). Like the Chihuahua pine, this species is not grazed by stock except in cases of starvation, but it is greatly injured by cattle which run over it to brush off flies (fig. 4). A considerable amount of cutting has been done to furnish mine timbers and fence posts.

This species does not show adventitious buds as does the pine, but when cut or broken off, it shows a much stronger tendency to produce pollard sprouts or stump sprouts than does the pine, and usually shows fully as strong a development of root collar sprouts. Out of 50 cases

noted near Oro Blanco in Cedar Creek Canyon, where the trees range from 20-30 cm. in diameter at breast-height, 39 showed vigorous sprouting. The trees had been cut by the axe, and the stumps were 30-75 cm. in height. In this canyon a count of 100 trees, broken off by cattle, which had stump diameters of 2.5-5 cm., produced very strong sprouts, with the exception of two trees which had been killed outright. The sprouts ranged from 15 to 120 cm. in height, according to age, site, vigor of tree, and number of sprouts to the stump. The most noteworthy example was a stump 1 meter tall, 25 cm. top diameter, which had produced 3 sprouts from the top of the stump. These sprouts were 2 meters tall and had basal diameters of 3.75-6.25 cm.

On the west slope of the Patagonia Mountains another count of 50 stools showed only 6 failures; 4 were stumps which were over 20 cm. in diameter, and 2 had been killed by fire. All stumps below 5 cm. in diameter were producing thrifty sprouts. Two stumps 15 cm. in diameter and 30 cm. tall were producing respectively 63 and 166 sprouts, while a third stump 12.5 cm. in diameter and 35 cm. tall was supporting 256 sprouts. Generally 3-10 sprouts are produced on each stool, and not more than 1-3 of the sprouts continue to live and grow to tree size.

In Belmont Gulch, fully 95 per cent of all reproduction of alligator juniper showed serious injury by livestock, which was almost invariably followed by sprout recuperation. In the vicinity of the Mowry Mine and in the Huachuca Mountains the injury to reproduction varied from 80 to 100 per cent. Throughout the entire region examined, the species showed its ability to reproduce by coppice, especially when the trees were less than 20 or 22.5 cm. in diameter.



FIG. 4.—Sprouts on alligator juniper as a result of grazing; collected near Flux Canyon.

A few cases were noted where sprouts were producing fruit at a very young age. On the west side of the Patagonias, a stump 15 cm. tall and 0.6 cm. top diameter had produced a sprout 1.8 meters tall and 2.5 cm. base diameter. This sprout bore 14 fully formed berries. Again, near the mountain pass on the main road between Washington Mine and Nogales, several side branches had been cut from the crown of a mature alligator juniper, and the resulting sprouts, which were 8-13 years old, ranged from 30 to 60 cm. in length. Many of them were loaded with fully formed fruits.

The sprouting ability of both these species is a controlling influence in maintaining a satisfactory reproduction in this region. Many sprouts of Chihuahua pine were found which were 10-15 cm. base diameter and 4.5-6 meters tall, and a few were found 20-22.5 cm. base diameter and 9-10.5 meters tall. Many alligator juniper sprouts were noted which were 7.5-10 cm. at the base and 4.5-4.8 meters tall. All sprouts on both species are still making a thrifty growth.—F. J. PHILLIPS, *The University of Nebraska, Lincoln*.

CELL DIVISION IN LYNGBYA

(PRELIMINARY NOTE)

The form here described is a large salt water species occurring at Cold Spring Harbor, L.I., and answers to the description of *Lyngbya majuscula*. In a cell of *Lyngbya* there is a large central body or nucleus, which in the stages between divisions is, except for the absence of a limiting membrane, much like the resting nuclei of the higher plants. The nucleus contains a mesh of fine fibers along which small granules are scattered. The mesh is imbedded in a clear substance resembling nuclear sap. When treated with either Haidenhain's hematoxylon or Flemming's triple, the mesh stains like linin and the granules like chromatin. Although there is no membrane or definite boundary around the nucleus, it is quite distinct from the surrounding cytoplasm. The above description is quite similar to that which OLIVE¹ gives of the nuclei of some of the Cyanophyceae studied by him.

As a cell of *Lyngbya* approaches division, fine fibers appear around the nucleus in a plane perpendicular to the longitudinal axis of the filament. These fibers, which have an appearance closely similar to that of the spindle fibers of other plants, are very numerous, and run from

¹ OLIVE, E. W., Mitotic division of the nuclei of the Cyanophyceae. Beih. Bot. Centralbl. 18:9-44. 1905.

the nucleus to the outer limits of the cytoplasm. They are all in practically the same plane, and thus form a plate across the center of the cell in the place where the cross wall, between the daughter cells, is to be produced. In several of his figures OLIVE shows fibers which appear quite like these. The stage just described, indeed, bears a close resemblance to his figs. 24-26 of *Oscillatoria*. However, since he does not describe these fibers in his text, or show them in longitudinal section, we cannot be sure how similar they are to those in *Lyngbya*.

At the end of each fiber in *Lyngbya*, there is laid down, against the cell wall, a small granule which stains black with Haidenhain's hematoxylin. These granules increase in size until they coalesce to form a ring around the center of the cell. This ring marks the place where the cross wall is to be formed, and it can still be seen, around the edge of this wall, after the wall has grown completely across the cell.

The production, at the place where the wall is to appear, of this ring by the fusion of granules formed at the ends of fibers which extend from the nucleus, would seem to indicate that the nucleus plays an important part in the formation of the wall, and that the nuclei of the Cyanophyceae may have functions similar to those of the nuclei of other plants. The presence of the fibers may indicate paths of conduction from the nucleus to the cell wall. DAVIS² describes a similar relation between the nucleus and the formation of the blepharoplast in the spores of *Derbesia*. Here strands radiate from the nucleus to the plasma membrane in the form of a funnel. According to this writer, "granules may be found on these strands apparently moving outwards towards the plasma membrane. These numerous granules accumulate in a circle just underneath the plasma membrane and fuse with one another to form a deeply staining firm ring, which is the blepharoplast."

In this discussion the central body of *Lyngbya* has been called a nucleus. This interpretation would seem to be justified by its structure and its relation to the formation of the cross wall.

The writer is indebted to Professor D. S. JOHNSON, in whose laboratory at the Johns Hopkins University the work was carried on, for material, and for other courtesies.—WILLIAM H. BROWN, *Michigan Agricultural College, East Lansing, Mich.*

² DAVIS, B. M., Spore formation in *Derbesia*. *Annals of Botany* 22:1-20. 1908.

CURRENT LITERATURE

BOOK REVIEWS

Intracellular pangenesis

DEVRIES'S *Intracellulare Pangenesis*, originally published in German in 1889, occupies an important position in the history of modern biology. It represents the fundamental speculations which guided the author in the experiments afterward reported in his great work *Die Mutationstheorie*, and it was also the first discussion presenting approximately the modern conception of unit characters.

Few scientists at the present time can accept in detail the scheme by which DEVRIES at that time explained the facts of heredity, but all appreciate the great value of this book in directing work along experimental lines, first by DEVRIES himself, and after him by a great number of both botanists and zoologists. While this work can scarcely be considered as having more than a historical significance at the present time, the triumph of the general principles introduced by it impresses the propriety of an English translation at the present time. This translation¹ has been satisfactorily made by GAGER. The translator points out in a brief preface the genetic relationship of "Intracellular pangenesis" to scientific conceptions now fully established upon an experimental basis.

A brief "Foreword" by STRASBURGER acknowledges his own indebtedness to the stimulating influence of DEVRIES, and observes that in a number of instances the speculative writings of that author both in *Intracellulare Pangenesis* and in the appended essay on *Befruchtung und Bastardirung* have proved prophetic of phenomena afterward actually found.

The translator has added occasional brief footnotes to explain certain allusions made by the author, or to call attention to more recent discoveries bearing upon the points under discussion. Several paragraphs have been omitted because there is no longer any necessity for speculation regarding the subject matter of those paragraphs. Purely as a historical work, the omission of these paragraphs seems to the reviewer to have been a mistake. It was impossible as well as undesirable to make the book contemporary science, though the desire to approximate this was undoubtedly the motive of the author and translator in making the omissions from the original work. Taking the place of these omitted paragraphs, the subjects involved in them are

¹ DEVRIES, H., *Intracellular pangenesis*, including a paper on fertilization and hybridization. Translated from the German by C. STUART GAGER. pp. xiii+270. Chicago: The Open Court Publishing Co. 1910.

treated in a paper on fertilization and hybridization read in Haarlem, Holland, by the same author in 1903. This essay is also modified from the original, being somewhat extended and brought more nearly down to date. It occupies the last 40 pages of the book, and presents a simple and interesting statement of the relation between modern cytological and genetic investigations as bearing upon the problem of unit characters.

Even in the brief time since this paper was revised for incorporation into this book, some of its subject matter has been given interpretations which render it unavailable for the particular application made, so that in at least one point it would need to be fundamentally rewritten. I refer particularly to the fact that the behavior of *Cytisus Adami* is taken as one of the clearest and simplest examples for demonstrating the existence of unit characters. Owing to the work of WINKLER and BAUR,² we now have a conception of this and other so-called graft hybrids which rules them out as examples of segregating unit characters.

Despite the fact that the book is neither strictly modern nor perfectly historical, it will be read with much profit by those interested in the subject of heredity and evolution, and all such will appreciate the work of GAGER in making this classic piece of speculation available to English readers.—GEO. H. SHULL.

A plant physiology

A treatise on plant physiology written by LECLERC DU SABLON³ has many features of interest. One is impressed by the definite, concrete treatment of the subject. When a topic is considered, a great worker in that line is selected and his methods and results clearly stated. This leaves the student with a clear idea of the results, and how they were obtained. This method certainly has advantages over the usually concise but rather abstract statements for beginning students, and it might be desirable to have such a treatise in English. However, a statement of this kind must necessarily have its shortcomings, and they are unnecessarily increased in this work. It must omit many contributions, and this is shown in the present work by the preponderance of attention given to French investigators. French students using the text would probably conclude that France has been leading in plant physiology, and that SABLON is by no means the least of the producers.

The book can in no sense be considered critical. This objection the author answers by saying that he intentionally avoids unsettled questions and devotes the space to the well established phases of the subject. One is forced to believe that he could have given a more modern statement without running

² For an excellent review of the recent work on graft hybrids and chimeras, see BOTANICAL GAZETTE for February 1911.

³ SABLON, LECLERC DU, *Traité du physiologie végétale et agricole*. vi+610. Paris: J. B. Bailliere et Fils. 1911.

unduly into unsettled questions. It would seem, for example, that a modern treatise on the subject ought to make some use of the masterly contributions of BROWN and ESCOMBE on the energy and material exchanges of the green leaf, and of FITTING's telling work on geotropism.

The order of treatment differs from that of most English and German works. The headings of the chapters are as follows: (1) nutritive reserves; (2) respiration; (3) fermentation; (4) assimilation of carbon; (5) mineral nutrition; (6) circulation of water; (7) transpiration; (8) latent life and development; (9) movements; (10) influences of environment; (11) physiology of the species.

The agricultural significance of the subject is emphasized. In the main this is done by using data gained from a study of the economic plants. The book is not indexed, but this is partly cared for by a full table of contents.—
WILLIAM CROCKER.

MINOR NOTICES

Das Pflanzenreich.⁴—Part 43 contains the first portion of a monographic treatment of the Umbelliferae by Dr. HERMANN WOLFF. The present part includes 9 genera of the tribes *Apioideae* and the heteroclitus *Ammineae*, to which are referred about 150 species. The body of the publication is occupied mainly with the genus *Bupleurum*, which is represented by approximately 100 species, nearly all occurring in the northern hemisphere. One new genus (*Ledebouriella*) is proposed, being based on *Rumia multiflora* Ledeb. of uncertain native habitat and *R. seseloides* Hoff. from the Altai.

Part 44 continues the elaboration of the Euphorbiaceae by Professor F. PAX and concerns only the tribe *Adrianeae*. The author recognizes 8 genera and 144 species, of which 34 are new to science. One new genus (*Cephalocrotonopsis*) is described, founded on *Cephalocroton socotranus* Balf. f. from the steppes of northern Africa. Of the 8 genera constituting the tribe, the genus *Manihot* comprises by far the largest number of species (129), and these have their center of distribution in Brazil.

Part 45 is devoted to a monographic consideration of the tribe *Dendrobiinae* of the Orchidaceae by the noted specialist Professor FR. KRÄNZLIN. Seven genera are elaborated, the first in importance being *Dendrobium*. This genus, as here treated, includes approximately 600 species, numerous varieties, and over 80 hybrids; and its greatest specific diversity is in the Monsoon region of the Old World. The genus is divided into ten subgenera which are

⁴ ENGLER, A., Das Pflanzenreich. Heft 43 (IV. 228). Umbelliferae-Apioideae-Bupleurum, Trinia et reliquae Ammineae heteroclitae von HERMANN WOLFF. pp. 214. figs. 24 (155). M 10.80. Heft 44 (IV. 147. II). Euphorbiaceae-Adrianeae von F. PAX. pp. 111. figs. 35 (151). M 5.70. Heft 45 (IV. 50. II. B. 21). Orchidaceae-Monandreae-Dendrobiinae von FR. KRÄNZLIN. pp. 382. figs. 35 (327). M 19.20. Leipzig: Wilhelm Engelmann. 1910.

based on the general character of the stems, leaves, and inflorescence. About 50 of the species recorded are new to science. The excellent keys, full descriptions, and numerous habital and detailed illustrations render this an exceedingly important treatise on a most difficult but highly interesting group of plants.—J. M. GREENMAN.

The Australian pines.—An elaborate volume records the results of the labors of BAKER and SMITH⁵ in studying the "pines of Australia." Curiously enough, there are no pines in Australia, the Abietineae being the only one of the six tribes of conifers unrepresented. The feature of the book is the wealth of illustrations, almost all of which are reproductions of photographs, many of which were made by the natural color process. The technical skill shown in this photographic work is to be highly commended, and probably in no other publication have conifers such a setting. The motive of the work is confessedly economic, and this aspect of the Australian conifers is doubtless presented with a completeness that leaves little to be desired. It seems that *Callitris*, next to *Eucalyptus*, is the most important genus of Australian trees; and the authors have indicated its complete generic separation from *Widdringtonia* of South Africa and *Tetraclinis* of North Africa, which makes it a genus restricted to Australia and Tasmania. In presenting the eleven genera of the region, the authors include so many details of structure and of products that the volume is a thesaurus of observations for those who are in a position to estimate their value. In the presentation of each species, after an account of its history and its taxonomic characters, there are described fully the economics, anatomy, and chemistry of leaves, fruits, timber, and bark.—J. M. C.

Conservation.—Because of the loose talk current concerning the conservation of our resources, it is well to have an authoritative treatise on the subject by one of acknowledged competence. Such a treatise is the one from the hand of President VAN HISE of the University of Wisconsin,⁶ which is based on lectures before students. Botanists will be interested especially in the chapter on forests, and in the one on land, in which soil conservation is considered. The author's expert training as a geologist fits him peculiarly for his consideration of the mineral resources, and scarcely less so for his treatment of the soils. The final chapter deals with conservation and mankind, and there are three appendices, which give declarations of conservation principles as set forth by various organizations.—H. C. COWLES.

⁵ BAKER, RICHARD T., and SMITH HENRY, G., A research on the pines of Australia. Technological Museum, New South Wales. 4to. pp. xiv+458. *figs.* 300. *maps* 3. Sydney: Government Printer. 1910.

⁶ VAN HISE, C. R., The conservation of natural resources in the United States. 8vo. pp. xiv+413. *pls.* 16. New York: The Macmillan Co. 1910. \$2.00.

Natürlichen Pflanzenfamilien.⁷—Parts 241 and 242 continue the supplement to the algae. One new genus (*Pseudolithoderma*) of the Lithodermataceae is proposed, which is based on *Lithoderma fatiscens* Kuck. not Aresch.—J. M. GREENMAN.

NOTES FOR STUDENTS

Current taxonomic literature.—J. C. ARTHUR (Bull. Torr. Bot. Club 37:569-580. 1910) under the title "New species of Uredineae VII" has described 13 new species.—H. H. BARTLETT (U.S. Dept. Agr. Bur. Pl. Ind. Bull. No. 189. pp. 29. 1910) presents the results of a study of the *Dioscoreae* of the United States, and in a detailed synopsis recognizes 5 species, 2 of which and one variety are new to science.—M. BOULY de LESDAIN (Bull. Soc. Bot. Fr. IV. 10:460-463. 1910) has published several new species of lichens, including 2 from Mexico.—E. BRAINERD (Bull. Torr. Bot. Club 37:523-528. pls. 34, 35. 1910) has described 5 new species of the genus *Viola* from the southern states.—V. F. BROTHERUS (Phil. Journ. Sci. Bot. 5:137-162. 1910) in a third "Contribution to the bryological flora of the Philippines" enumerates 91 genera and 143 species; one monotypic genus (*Pseudoracelopus*) and 27 species belonging to several different genera are recorded as new.—C. DECANDOLLE (Leaflet. Phil. Bot. 3:759-789. 1910) under the title "Philippine Piperaceae" records 50 recognizably distinct species, varieties, and forms of *Peperomia* and *Piper*, more than one-half of which are new to science.—J. CARDOT (Rev. Bryol. 37:65-72. 1910) in an article entitled "Diagnoses préliminaires de Mousses mexicaines" has published several new species.—E. B. COPELAND (Phil. Journ. Sci. Bot. 5:283-285. 1910) in an article entitled "Additions to the Bornean fern flora" has published a variety and several new species of ferns, and proposes a new genus (*Protolindsaya*).—H. N. DIXON (Journ. Bot. 48:297-310. pls. 507, 508. 1910) presents a paper on Indian mosses and includes several species new to science. One new genus (*Merceyopsis*) of the Pottiaceae is characterized, which is said to be intermediate between *Merceya* and *Hyophila*, and is represented by 7 known species.—S. T. DUNN (Kew Bull. 386, 387. 1910) has published a new genus (*Leptoderris*) of the Leguminosae from tropical Africa, and gives a key to the 14 known species.—A. D. E. ELMER (Leaflet. Phil. Bot. 2:703-728. 1910) records 30 species of Lauraceae from Mt. Apo and Mt. Giting-Giting, P.I., 18 of which are designated as new. The same author (*ibid.* 729-734) lists 6 species of *Solanum* from Mt. Apo, of which 4 are new; and (*ibid.* 735-740) describes 5 new species of the genus *Begonia* from the Philippines.—J. S. GAMBLE (Kew Bull. 218-228. 1910) in

⁷ ENGLER, A., and PRANTL, K., Die natürlichen Pflanzenfamilien, etc. 241. und 242. Lieferungen. Chlorophyceae von N. WILLE. Phaeophyceae und Dictyotales von F. R. KJELLMAN und N. SVEDELIUS. Rhodophyceae von N. SVEDELIUS. Nachträge zum I. Theil, 2. Ab. pp. 97-192. figs. 54 (174). Leipzig: Wilhelm Engelmann. 1910. M 6.

a paper on "New Lauraceae from the Malayan Region II" includes the description of a new genus (*Stemmatodaphne*). The same author (Phil. Journ. Sci. Bot. 5:267-281. 1910) under the title "Bamboos of the Philippine Islands" enumerates 7 genera to which are referred 25 species, 12 being new to science.—A. O. GARRETT (Mycologia 2:265-304. 1910) in an article entitled "The smuts and rusts of Utah" publishes a catalogue of these plants collected in seven different counties of Utah, during eight years of field work, recording 144 species.—M. GÜRKE (Monats. für Kakteenkunde 20:145-148. 1910) characterizes a new species of *Cereus* (*C. pseudosonorensis*); the plant has been brought into cultivation in European gardens along with *C. sonorensis* from Mexico.—E. HACKEL (Rep. Nov. Sp. 8:513-523. 1910) has published several new species of Gramineae, 5 of which are from Mexico and South America. The author also describes a new monotypic genus (*Anelytrum*), found near Genoa, Italy, the native habitat of which is still in doubt.—H. HARMS (Bot. Jahrb. 45:293-316. 1910) under the heading "Leguminosae africanae V" has published 27 new species and records two genera (*Eurypetalum* and *Tessmannia*) new to science.—E. HASSLER (Rep. Nov. Sp. 8:552-560. 1910) continues the enumeration of plants of Paraguay, publishing several new species and varieties in the Leguminosae.—A. A. HELLER (Muhlenbergia 6:97-113. 1910) gives further results of his studies of "The Nevada lupines" and describes two new species (*L. montigenus* and *L. nevadensis*).—J. HERZOG (Beih. Bot. Centralbl. 27²:348-358. 1910) has published 11 new species of mosses from Bolivia.—B. P. G. HOCHREUTINER (Bull. N.Y. Bot. Gard. 6:262-299. 1910) under the title "Critical notes on new or little known species in the Herbarium of the New York Botanical Garden" has published 27 new species and varieties of flowering plants, mostly from South America.—J. HUBER (Bol. Mus. Goeldi 6:60-90. 1910) in an article entitled "Novitates florum Amazonicae" has published 31 new species of flowering plants from the region of the Amazon; the paper includes a new genus (*Euxylophora*) of the Rutaceae.—F. KRÄNZLIN (Rep. Nov. Sp. 8:545. 1910) has published a new species of *Cleisostoma* (*C. chrysochilum*) from the Philippines.—G. LISTER (Journ. Bot. 48:310-312. 1910) has described a new genus (*Colloderma*) belonging to the Mycetozoa; it is based on *Didymium oculatum* Lippert, which was originally found in upper Austria and rediscovered near Skene, Aberdeenshire, Scotland.—J. LUNELL (Am. Mid. Nat. 1:204-208, 233-238. 1910) has described 7 new species and several varieties of spermatophytes from North Dakota.—K. K. MACKENZIE (Torreya 10:249, 250. 1910) records a new species of *Proserpinaca* (*P. intermedia*) at present known only from New Jersey and Georgia, and (*ibid.* 228-230) a new blueberry (*Vaccinium caesariense*) from New Jersey.—P. MAGNUS (Ber. Deutsch. Bot. Gesell. 28:377-380. pl. 11. 1910) describes and illustrates a hitherto unknown parasitic fungus from the Transvaal; the fungus was found on stems of *Zizyphus* and a new genus has been created for it, namely *Hyalodema*.—G. MASSEE (Kew Bull. 249-253. 1910) describes several new fungi and includes a new *Merasmus* from Trini-

dad, a new *Polyporus* from Louisiana, and a new genus (*Pilula*) from tropical Africa.—E. D. MERRILL (Phil. Journ. Sci. Bot. 5:1-136. 1910) has published an "Enumeration of Philippine Leguminosae with keys to the genera and species," recognizing 90 genera and about 280 species of this family in the Philippine Islands; one new genus (*Monarthrocarpus*) is proposed, being based on *Desmodium securiforme* Benth; 15 species and 4 varieties are new to science and several new combinations are made. The same author (*ibid.* 167-257) under the title "New or noteworthy Philippine plants VIII" has published 104 new species of flowering plants and proposes the following new genera: *Curraniodendron* of the Saxifragaceae, *Astrocalyx* and *Cephalomedinella* of the Melastomaceae, and *Pygmaeopremna* of the Verbenaceae.—E. D. MERRILL and M. L. MERRITT (*ibid.* 287-370) begin a consideration of "The flora of Mount Pulog," one of the highest mountains of the Island of Luzon. The present article gives a general descriptive account of the island, characterizing four floral regions, or types of vegetation, and enumerates the plants from the Hepaticae to the Umbelliferae. The paper contains descriptions of two new genera (*Aniselytron* and *Monostachya*) of the Gramineae and 21 new species belonging to different genera of flowering plants.—W. A. MURRILL (Mycologia 2:305. 1910) has described a new boletus (*Gyroporus jamaicensis*) from Jamaica.—J. A. NIEUWLAND (Am. Mid. Nat. 1:263, 264. 1910) proposes a new genus (*Bataprine*) based on *Galium hispidulum* Michx.—C. H. OSTENFELD (Ber. Deutsch. Bot. Gesell. 28:397-400. 1910) has published a new genus (*Thorosphaera*) of the Cocolithophoraceae; the material on which the genus is based was collected in the Mediterranean Sea near Calabria.—S. B. PARISH (Muhlenbergia 6:113-128. 1910) presents a useful synopsis of "The Southern California Juncaceae" with keys to the genera and species.—F. PAX (Bot. Jahrb. 45:234-241. 1910) under the title "Euphorbiaceae africanae XI" has published several new species and characterizes two new genera, namely *Zimmermannia* and *Excoecariopsis*.—F. PETRAK (Beih. Bot. Centralbl. 27²:207-255. pls. 1, 2. 1910) under the title "Die mexikanischen und zentralamerikanischen Arten der Gattung *Cirsium*" presents an interesting revision of the group, recognizing 27 species. The study is based on the material in the Royal Museum of Natural History in Vienna.—L. QUEHL (Monats. für Kakteenkunde 20:149-150. 1910) describes and illustrates a new species of *Mamillaria* (*M. bombycina*) from Mexico.—A. REHDER (Mitt. Deutsch. Dendr. Gesell. 1910, pp. 248-254) in an article entitled "Einige neue und kritische Gehölze" publishes a hitherto unrecorded form of *Ribes Cynosbati* from Vermont and West Virginia, a new form of *Rosa pratincola* from Central United States, and three new hybrids in the genus *Hypericum*.—H. H. RUSBY (Bull. N.Y. Bot. Gard. 6:487-517. 1910) has described 67 new species of flowering plants from Bolivia, based on collections made by R. S. WILLIAMS in 1901 and 1902.—P. A. RYDBERG (Bull. Torr. Bot. Club 37:541-557. 1910) in continuation of his "Studies on the Rocky Mountain flora" has described 4 new species of *Carduus*.—C. S. SARGENT (Proc. Acad. Phila. 62:150-253. 1910)

under the title "Crataegus in Pennsylvania II" records 110 species of this genus from Pennsylvania, 79 of which are indicated as new.—R. SCHLECHTER (Rep. Nov. Sp. 8:561-572. 1910) under the title "Orchidaceae novae et criticae" has published 19 new species of orchids, several being from America; one new genus (*Platystele*) is proposed, which is based on PITTIER'S no. 2013 from Costa Rica.—J. K. SMALL (Torreya 10:230, 231. 1910) has described a new species of *Anychiastrum* (*A. montanum*) from the mountains of southern Pennsylvania to Georgia.—I. URBAN (Symb. Ant. 4:353-528. 1910) continues the "Flora portoricensis." The present fascicle contains the genera from *Euphorbia* to *Verbena* and includes a new species of *Heliotropium* (*H. antillanum*) from Porto Rico and Cuba, and a new variety of *Jussiaea suffruticosa* L.—W. WEINGART (Monats. für Kakteenkunde 20:161, 162. 1910) has published a new species of *Cereus* (*C. cinnabarinus* Eichlam) from Guatemala.—R. S. WILLIAMS (Bull. N.Y. Bot. Gard. 6:227-261. 1910) in a second contribution on Bolivian mosses records approximately 200 species and varieties, and of these 19 are described as new.—H. L. WILSON (Univ. Calif. Pub. Bot. 4:75-84. pls. 12, 13. 1910) in conjunction with W. A. SETCHELL has published a new genus (*Gracilariophila*) parasitic on *Gracilaria confervoides*. The host and parasite have the same subordinal relationship.—H. WINKLER (Bot. Jahrb. 44:497-571. 1910) has published the first of a series of articles entitled "Beiträge zur Kenntniss der Flora und Pflanzengeographie von Borneo." The paper is based mainly on collections made by WINKLER in 1908, and in the work of identification the author has been assisted by eminent specialists. About 45 new species are here described for the first time, and one new genus (*Campanocalyx*) of the Rubiaceae is included.—H. WOLFF (Rep. Nov. Sp. 8:524-526. 1910) under the title "Umbelliferae novae I" has described new species from Mexico and China.—Different authors (Kew Bull. 328-344, 368-371, 381-386. 1910) have published new species of flowering plants, chiefly from Africa but including several from Peru. One new African genus (*Necepsia*), belonging to the tribe *Crotoneae* of the Euphorbiaceae, is proposed by D. PRAIN.—J. M. GREENMAN.

Algal coals.—The characteristic petroleum-yielding coals known as bog-head, cannel, etc., have been referred to an algal origin by RENAULT, BERTRAND, and POTONIÉ, a view that has been more or less acceptable to our own students of paleozoic coals. The evidence of such an origin is the occurrence in such coals, as well as in bituminous schists and oil-shales, of abundant "spherical or oval bodies, often arranged in layers," these bodies being interpreted as colonial algae. They have now been investigated by JEFFREY,⁸ who developed a special technique to secure numerous and even serial thin sections. As a consequence, the structure and hence the nature of these bodies have been brought out with a clearness not heretofore possible.

⁸ JEFFREY, E. C., The nature of some supposed algal coals. Proc. Amer. Acad. 46:273-290. pls. 5. 1910.

They are certainly not algae, but spores of pteridophytes, a group which constituted an important part of the paleozoic vascular flora, and which has always been regarded as responsible, to a large extent at least, for the ordinary coals. This conclusion sets aside the algal hypothesis of the origin of petroleum and other substances, and refers such products to the waxy and resinous spores of pteridophytes, "laid down on the bottoms of the shallow lakes of the Coal Period. These lacustrine layers, either as cannels, bog-heads, or bituminous shales, according to the sporal composition and the admixture of earthy matter, are the mother substance of petroleum. Pressure and temperature, either separately or combined, in the presence of permeable strata, have brought about the distillation of petroleum from such deposits."—J. M. C.

Alkaloids and algae.—COMÈRE⁹ finds that some alkaloids can be used by algae as the only source of nitrogen. The algae used were *Ulothrix subtilis* and *Spirogyra crassa*, and the alkaloids were morphine hydrogen chloride, atropine sulphate, cocaine hydrogen chloride, quinine hydrogen chloride, and strychnine sulphate. The alkaloids were added gradually as assimilated, so that the plants were never subjected to strong solutions. *Ulothrix* proved to be far more amenable to cultural conditions than *Spirogyra*. It can readily assimilate morphine and atropine, and less readily cocaine; *Spirogyra* showed less marked assimilation of these compounds. Quinine could not be assimilated by either, and strychnine was very toxic to both, even in great dilution. Some of the alkaloids, therefore, are not aplastic.—WILLIAM CROCKER.

Response to light.—DANGEARD¹⁰ finds that in three species of *Chromatium* studied (*C. Okenii*, *C. vinosum*, *C. sp. ?*) there is a marked accumulation in the longer rays of the spectrum as observed by ENGELMANN. In the infra-red there are two regions of accumulation; one in ray lengths 0.840–0.820 μ , and the second at 0.800–0.790 μ . In the visible spectrum there is a zone of accumulation between the *B* and *C* lines, and a second one extending to each side of the *D* line. A green bacterium that he recently described also responds to longer rays; it accumulates in a zone with ray lengths 0.770–0.670 μ . Some other experiments, claimed to show the relatively great effectiveness of long rays in assimilation and growth, add nothing of value to our knowledge.—WILLIAM CROCKER.

⁹ COMÈRE, JOSEPH, Du rôle des alcaloïdes dans la nutrition des algues. Bull. Soc. Bot. France 57:277–280. 1910.

¹⁰ DANGEARD, P. A., Phototactisme, assimilation, phénomènes de croissance. Bull. Soc. Bot. France 57:315–319. 1910.

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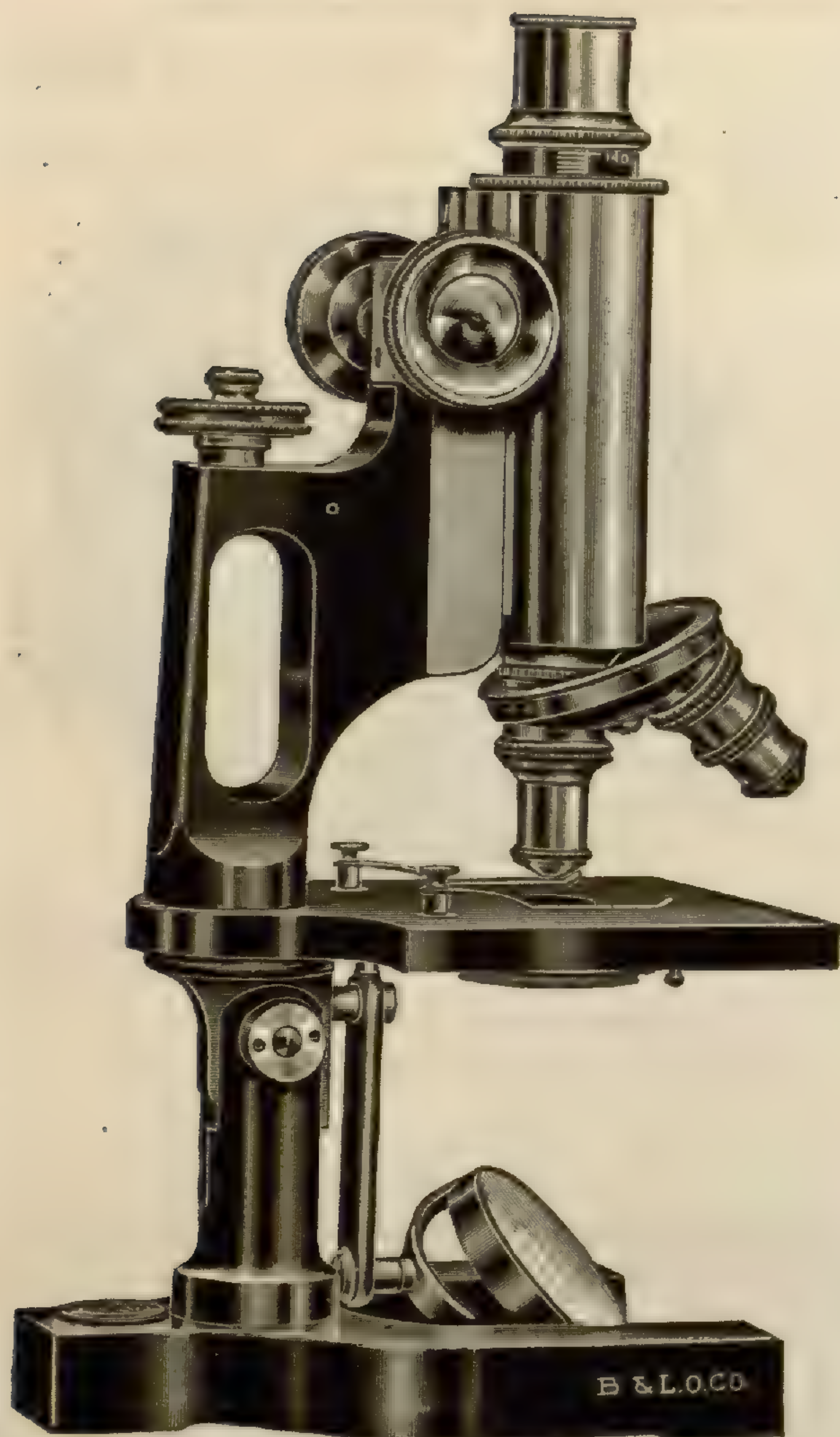
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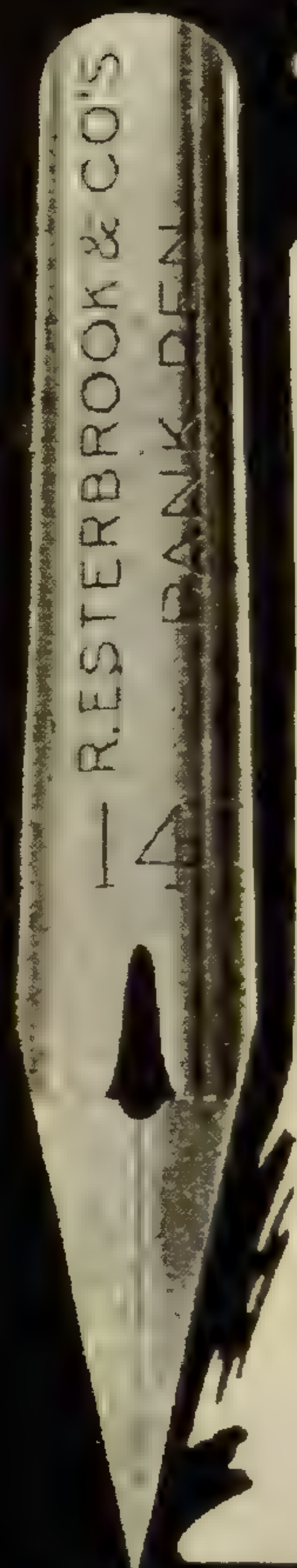
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THE BOTANICAL GAZETTE

JUNE 1911

CELL AND NUCLEAR DIVISION IN CLOSTERIUM

B. F. LUTMAN

(WITH PLATES XXII AND XXIII AND ONE FIGURE)

Historical

The first figures showing division in desmids were those of *Cosmarium* by EHRENBURG (11). Those drawings, while not entirely accurate, indicate clearly that he saw the two new daughter half-cells being interpolated between the old ones. Each half of the parent cell was evidently considered by him as an individual, since his genus description states that the individuals are arranged in the colonies "in chains of two or four."

NÄGELI (33), RALFS (35), and FOCKE (17) observed cell division in the desmids and gave fairly complete accounts of the process. DEBARY (9) did not describe division in detail, but mentions the fact that the newly formed transverse wall of *Closterium* and *Penium* is flat, and that the new end grows out as a cone-shaped structure. As the chromatophore is divided into two parts, some of the older observers, as EHRENBURG, regarded the mature plant as a chain of two cells, but DEBARY was clear on this point and recognized the desmid as a single cell with a nucleus between the halves. Nothing was observed by any of these investigators as to the conduct of the nucleus during division, as the importance of that organ of the cell was not yet fully recognized.

It is to ALFRED FISCHER (14) that we owe our first knowledge of the details of the process as it occurs in this genus. FISCHER found the cross-wall formed in essentially the same manner that STRASBURGER had described for *Spirogyra*. It appears soon after

nuclear division, at the middle of the cell at the point where the old nucleus lay, and cuts across the cell at right angles to its long axis. It is only after the complete isolation of the two halves of the old cell that the new ends of each *Closterium* grow out again to restore the symmetry of the chromatophore and cell outline in each individual. In each new end there lies a dense accumulation of cytoplasm, and in this is the daughter nucleus. FISCHER saw that immediately after nuclear division the daughter nuclei move back from the position occupied by the mother nucleus. They migrate out at right angles to the long axis of the cell, and move back from the equator of the cell to their new position in the forming furrow of the chromatophore. FISCHER watched this process eight times in living specimens of *C. Delpontii*, and found that the migration is a very rapid one and may occur along either the convex or concave side. In *C. Delpontii* this migration had frequently been completed before the two cells had pulled apart, and in *C. moniliferum* the nucleus frequently came to rest in the furrow in the chromatophore before that body had been entirely divided, the latter part of the process seeming to be completed under its direction. In the passage backward around the chromatophore the nucleus seems to press that body to one side to make room for it to pass. The granular protoplasm that had gathered at the middle of the mother cell forms the tip of each new half, and apparently assists as MOLL'S embryonic substance in the very rapid growth of the new membrane. This new half rounds out, the protoplasm streams into it, and the plant soon takes on a symmetrical shape. The new end vacuole appears in the granular tip, which even in the adult remains without chlorophyll. In *C. Delpontii* the entire process, beginning at about midnight, was completed and the two halves had become symmetrical in about five hours. FISCHER points out the further interesting fact that in the young *Closterium* the chromatophore in either end grows so that the two halves become pressed on each other, forming an apparent, but of course not real, fusion, as the two halves of the chromatophore remain separate throughout the life of the individual. He also noted that these observations on cell division give the reason for the conformity of the ridges of the chromatophore on either side of the nucleus.

FISCHER (15) in a later paper gave further details as to the origin in the new half of the end vacuoles and its crystals. He believed that the latter formed in the cytoplasm and later migrated into the vacuole.

Some of FISCHER's observations on the method in which the cell wall divides were criticized by both GAY (18) and HAUPTFLEISCH (23). GAY's paper I have not seen, but according to HAUPTFLEISCH, who reviews it, he points out that FISCHER's results hold only for wall division in those varieties with thick walls on which were longitudinal and cross-markings. HAUPTFLEISCH showed further that in those forms without girdle rings, such as *C. Ehrenbergii* and *C. moniliferum*, the isolation of the daughter cells is accomplished by a simple splitting of the cross-wall.

Considerable work has been done by LÜTKEMÜLLER (26) on the formation of the cell wall during the division process, but as little of his work has direct bearing on division in the species discussed in this paper, it will not be reviewed. Based on this work, LÜTKEMÜLLER has attempted to formulate a consistent scheme of phylogeny for the desmid group. He regards them as degenerate filamentous conjugates. This view he shares with WEST (46), who, as a result of studies on variation in desmids, had published an almost identical theory of their phylogeny three years previously.

The very peculiar nucleus of the desmids was evidently a puzzle to the early observers. DEBARY (9) does not attempt to describe it, but BRAUN (5) has the following to say: "The nucleus, with its colorless mucilaginous envelope, is maintained in the center of the spindle-shaped cell by the green lamellae of contents, arranged radiantly around the long axis of cell, which lamellae are interrupted by it in the middle of the cell." From this it will be seen that he evidently regarded the central granular mass as the nucleus, while the nuclear reticulum was the "mucilaginous envelope."

I have described (27) the resting cell of *Closterium* with special reference to the chromatophore and pyrenoids, but have given also briefly some idea of the peculiar structure of the nuclei in *C. Ehrenbergii* and *C. moniliferum*. The particular feature to which I called attention was the great accumulation of stainable material

at the center of the nucleus, which seemed to take the place of the nucleus or nucleoli of other plants.

All of this work on *Closterium*, with the exception of my investigation, it will be noted has been done either on the living cells or on fixed and stained whole mounts. The only members of the Conjugatae that have been studied with reference to cell and nuclear division in sectioned material are *Spirogyra* and *Zygnema*. Many investigators, on account of the ease with which the nuclear process can be followed in the filament, have preferred to use fixed and stained but unsectioned filaments, but others have resorted to sectioned material as the best means for seeing the finer details of the nuclear phenomena.

In *Spirogyra*, as is well known, the nucleus contains one or more nucleoli that are proportionally exceedingly large. On account of the great mass of nucleolar material, it has been generally accepted that the network outside the nucleoli either was very poor in chromatin or was entirely free from it, the entire chromatic material being concentrated in the central bodies which have been termed the chromatin nucleoli. A dispute has centered around the origin of the chromosomes; whether they came from the reticulum around the nucleolus or from the nucleolus itself. From the time when STRASBURGER (37) first investigated divisions in *Spirogyra* to the latest paper by KARSTEN (25) on divisions in the young plant as it comes out of the zygospore, the opinions of the investigators as to the origin of the chromosomes have been divided. Altogether over twenty papers have appeared on the subject, making the nuclear divisions of *Spirogyra* the most thoroughly studied of those of any algal form.

In STRASBURGER'S original contribution, which appeared in *Zellbildung und Zelltheilung* (1875), he claimed that the nucleolus or nucleoli by first falling into granules, which arrange themselves at the middle of the spindle, form the plate. This view he modified in 1882 (37) when he returned again to the study of *Spirogyra*, then arriving at the conclusion that in the species he was studying (*S. majuscula*) there was a nuclear cavity, the ends of the chromatin loops being at the poles of the spindle. This structure forms the equatorial plate, the nucleolus in the meantime having disappeared

and its substance having been used up probably in the formation of this spireme. After metaphase the chromosomes form two new spiremes, one at either pole, in the midst of which the nucleoli reappear. In 1884, in *Spirogyra nitida*, STRASBURGER (38) observed that the spireme appeared close to the nucleolus, which as a result seemed to take on a granular corroded appearance. In his paper in 1888 (39) he finds that in *Spirogyra polytaeniata* a typical spireme, gradually becoming denser, is formed in the nuclear reticulum, while the nucleolus disappears about the end of its formation. Twelve chromosomes are formed, which during the telophase form new spiremes and become reticulated. In other words, at this time in this species of *Spirogyra*, STRASBURGER believed that the nucleoli do not behave very differently in mitosis from those of higher plants.

FLEMMING (16) considered the spireme to be formed partly from the material in the nucleolus which became arranged in it. The achromatic part of the reticulum is utilized in the formation of the spindle. TANGL (41) claimed that the equatorial plate arose directly from the nucleolus, while CARNOY (6) believed that all the chromatic material in the nucleus was collected in the nucleolus, forming there a still smaller body which he proposed calling the nucleo-nucleolus. The nuclear cavity surrounding this body was empty. MEUNIER (30) confirmed these observations, finding a spireme formed inside the nucleolus in the early prophases. In the reconstruction stages the achromatic basis of the nucleolus is established first, and then on this the chromatic substance is deposited.

ZACHARIAS (48), as a result of microchemical tests, considered the nucleolus as pure plastin and similar to that of the higher plants.

DEGAGNY (7) in 1890 believed that while there was chromatin both in the nucleolus and in the extra-nucleolar part of the nucleus, it was the nucleolus alone that formed the plate. In later papers, however, he changed this opinion, and derived the plate from the spireme which comes to envelop the nucleolus closely and seems to absorb the substance from it.

Both MOLL (32) and MITZKEWITCH (31), applying modern

cytological technic and using microtome sections, arrived at the conclusion that practically all the chromatin was centered in the nucleolus. MOLL found the chromatin coming out of the nucleolus, leaving the latter empty. This chromatin then formed a spireme which cut up into 12 chromosomes. MITZKEWITCH found in the nucleolus two constituents, chromatin and linin. The chromatin appeared in the early prophases of division in the form of a definite number (24) of bodies imbedded in a mass of more lightly staining linin. This mass occupies the position formerly held by the nucleolus, and apparently seems to have resulted from its transformation.

VAN WISSELINGH (42, 43, 44), by a process of progressive digestion of the various parts of the nucleus by 40 per cent chromic acid, came to the conclusion that the nucleolus contains chromatin. He also found chromatin in the surrounding reticulum. He ascribed the origin of only two of the chromosomes to the nucleoli; if there are two nucleoli one chromosome comes from each; the other ten arise from the nuclear reticulum.

BERGHS (2) has recently devoted a very long paper to a detailed account of the process as he finds it in a *Spirogyra* which he believes to be *S. nitida*. He finds all of the 12 chromosomes arising from the nucleolus, the reticulum surrounding it being entirely free from chromatin. After the chromosomes are formed, there still remains in the nucleolus a second substance which stains less deeply. This substance divides transversely into two groups of pieces which move to the poles with the chromosomes. The nucleus is reconstructed out of these two substances, which, after undergoing vacuolization, are condensed in the nucleolus.

KARSTEN (25) finds in the first division of the fusion nucleus in the zygospore of *Spirogyra jugalis* that 14 tetrads arise from the nucleolus, which lies surrounded by light plasma containing two or more weakly staining chromatin spheres, apparently comparable to the extruded nucleoli of other plants. He has followed the development of these chromosomes and finds them appearing gradually in the dark stained nucleolar mass. This stage he believes to be comparable to synapsis in the higher plants.

Miss MERRIMAN (29) finds in *Zygnema* a central body which

apparently gives rise to part of the chromosomes, the remainder coming from extra-nucleolar granules. In these opinions it will be seen that she agrees with the results of VAN WISSELINGH (43) on *Spirogyra*. At no time did she find a spireme formed. In the telophase, part of the chromosomes, the number apparently not having been determined, fuse to form this central body (nucleolus), while the remaining ones are distributed throughout the nuclear cavity as granules.

ESCOYEZ (12) has also recently studied *Zygnema* in GRÉGOIRE'S laboratory, and has arrived at quite different conclusions from those of Miss MERRIMAN. While the nucleolus is very large, the nuclear reticulum furnishes all the chromosomes. He does not deny the fact that the nucleolus may supply some of the chromatic material, but is certain that the morphological chromosomes do not come from it. He finds the chromosomes to arise, not by the fusion of granules as Miss MERRIMAN describes, but in the form of slender rods. In the telophase, the nucleolus is not formed by the union of the chromosomes at the center, but appears to arise independent of the chromatic reticulum.

The spindle in *Spirogyra* is believed by STRASBURGER (39), MITZKEWITCH (31), VAN WISSELINGH (44), and BERGHS (2) to be purely of cytoplasmic origin, while MEUNIER (30) thinks it to be partly so. On the other hand, FLEMMING (16) believed it to be derived from the nucleus itself. Miss MERRIMAN (29) seems to favor the view that the spindle arises intranuclearly in *Zygnema*. ESCOYEZ (12) believes that in *Zygnema* it is formed from the cytoplasm, although he has not followed the process in detail.

The very peculiar bodies, nucleolus or some structure corresponding to it, that are present in the resting nucleus of *Closterium*, I have described in my previous paper (27). On account of the importance of the question as to the behavior of these bodies in nuclear division, especially with reference to the theories of inheritance, which makes the chromatin or the chromosomes the special idioplasm, it will be well to notice some of the recent opinions relating to the rôle of the nucleolus in the formation of the chromosomes, especially in the higher plants.

WAGER (45) has recently quite thoroughly reviewed the litera-

ture on that subject, and has expressed some opinions of his own derived partly from the facts as they have been presented by various observers and partly as a result of his work on nuclear division in the root tip of *Phaseolus*. He arrives at the conclusion that the nucleolus is not an independent organ of the cell, but only a part of the nuclear thread in which a considerable portion of the chromatin may be stored, and from which it may be withdrawn again at the time of chromosome formation. He agrees with DIXON (10), therefore, that if the chromatin is the bearer of the hereditary qualities, not only the chromatin granules but also the nucleolus must be taken into account in any theories on the subject.

In a number of other plants outside of the Conjugatae the nucleolus has been reported as containing the larger part or all of the stainable material in the nucleus. GOLENKIN (19) finds in *Sphaeroplea* the nucleolus breaking up directly into chromosomes. WOLFE (47) describes all the chromatin in the *Nemalion* nucleus as being stored in the nucleolus. BEER (1) says that the nucleolus of the cells of the *Riccia* thallus contain practically all the chromatin. He was able also at times to distinguish in it a composite structure, as though it were composed of granules. He believes that the spireme thread becomes thickened by the material from these granules. He also believes that similar conditions are found in one of the mosses (*Funaria*).

ESCOYEZ (12) states that the nucleolus in *Stypocaulon* appears to contain the larger part of the chromatin, as the reticulum around it stains very lightly in the iron-alum-hematoxylin. The chromosomes are formed from the reticulum, however, and in the telophase the chromosomes form again a typical reticulum, the nucleolus not being formed by their fusion.

STRASBURGER (40), as a result of the fact that he finds in *Marsilia* practically all the stainable material collected in the nucleolus, draws the conclusion that the linin and not the chromatin may be the bearer of the hereditary qualities, while the division of the chromatin is only a device to equalize the food supply of the cells.

The very discrepant accounts of *Spirogyra* given by different investigators, and the very close relationship of *Closterium* to it, make a study of the latter very desirable, especially in view of the

very peculiar structure of the nucleolus as I have previously described it (27). If the chromosomes fuse together in the telophase of the divisions of the Conjugatae to form a large central body or bodies, this ought to be a favorable place to find them, for this mass is certainly a composite one.

This work was begun at the University of Wisconsin under the direction of Professor R. A. HARPER, but was completed after leaving his laboratory. I am since greatly indebted to him, however, for his critical reading of the manuscript of this paper and for his suggested changes.

Methods

I have already described in my previous paper (27) my method for fixing, imbedding, and sectioning *Closterium*, and will only refer briefly to it here. As had happened in the two preceding years, the lily tanks in the botanical greenhouse at the University of Wisconsin were rapidly becoming covered with *Closterium* on the bottom and sides in the early part of May 1909, the organisms occurring in such abundance that they could be obtained in quantity and under favorable conditions for the study of their asexual reproduction. They have regularly disappeared from the tanks during the winter, whether due to the water becoming cold or from their going into the resting condition could not be determined, but they have just as regularly begun to appear again in quantity about the middle of April. The first series of fixations was made the night of May 2, beginning at 11 P.M. and continuing hourly from that time until 5 A.M. Four other series were fixed during the month of May. It was found that the early stages of chromatophore and nuclear division occurred more frequently early in the evening, even as early as 9 P.M., so the major part of my work has been done on material obtained from that time until midnight. The time of the maximum number of divisions is undoubtedly dependent on the character of the preceding day, whether cloudy or bright, determining the amount of starch stored, and more especially on the temperature of the water, although no accurate observations were made on these factors.

The physiological condition of the individual plants also determines their ability to divide, the particular condition required

being apparently a chromatophore filled with large quantities of starch. The difference in external appearance between those cells which are dividing and those not dividing is very striking; the individuals whose pyrenoids only showed a thin shell of starch and in whose pale green chromatophore there was practically no stroma starch were never found dividing, while those whose pyrenoids were surrounded by thick pieces of starch and whose dark-green chromatophore contained an abundance of free starch were the ones found in division.

Fixation was in Flemming's weaker solution, half-strength, although other fluids were used. This solution caused some shrinkage, but as this was principally in the ends of the chromatophore, it did not affect the phenomena of the nuclear and cell division that were occurring principally at the middle of the cell. When the organisms had been brought into the paraffin in which it was desired to cut them, the previous changes of alcohol, paraffin, etc., having been made by pipetting off the liquid above the *Closterium* lying at the bottom of the vial, the vial containing them was held in ice water for a few minutes. The glass could then be broken away and the layer of paraffin containing the plants sectioned. Staining was largely with the triple stain, although iron-hematoxylin was used to a limited extent. After fixation in the Flemming solution all the nuclear and cytoplasmic structures take differential staining very easily.

In addition to the sectioned material, whole amounts were stained with iron-alum-hematoxylin, gradually transferred to glycerin from the water, and mounted in glycerin.

The same species, which I consider to be *Closterium Ehrenbergii* and *Closterium moniliferum*, whose vegetative cells were described in my previous paper (27), were found dividing. In my first series of fixations (May 2) both of these were very abundant, but in all my later attempts I succeeded in getting only *C. Ehrenbergii* in division in quantity, the *C. moniliferum* having in the meantime largely disappeared. As my later fixations were the richer in divisions and were the ones upon which I have depended for the larger part of my work, it was found possible to work out the process in all detail in sections in *C. moniliferum*, although I was able

to get a fairly complete series of stages of division in my whole mounts. Enough division figures were found in the sections, however, to assure me that the process was practically the same in the two species.

External appearance of the division process

FISCHER (14) has given a fairly complete description of the process of division as it can be seen both in the living specimens and in stained whole mounts, but in order to understand the structures and phenomena that are found in the sections it was necessary to restudy the whole process in detail, according to FISCHER's method. It will be remembered, too, that owing to the density of the chromatophore and the granular nature of the cytoplasm, FISCHER was able only to guess at the nuclear changes that were occurring simultaneously with those seen in the cytoplasm. Further, it is practically impossible with whole mounts to discover the details of the method by which the new cross-wall is put across the old cell.

Many species show parts of several generations in their cell walls. LÜTKEMÜLLER (26) has made a careful study of a number of these species and genera. In both *C. Ehrenbergii* and *C. moniliferum*, however, the process is a very simple one, and the wall, which is very thin and without markings, does not permit the distinction of the parts belonging to different cell generations.

The first external appearance of division in an individual is a pinching in of the chromatophore about a third of the distance from the middle to the tip (figs. 1-9). As previously noted, this occurs only in individuals that have their dark green chromatophores well filled with starch. This pinching in affects at first only the ridges of the chromatophore and occurs inside the plasma membrane, which becomes pulled away from the chromatophore. The mechanics of this process is difficult to understand. It is plain that the division of the chromatophore is entirely distinct from that of the cell. It has the appearance of being constricted as by a rubber band around it at this point. The division of the chromatophore in *Spirogyra* and other Conjugatae is described as due to the constriction of the entire cell. The chromatophore here would

seem to divide just as the entire cell divides in animals like the amoeba, but the constriction in these animals, it must be noted, is a constriction of the plasma membrane. In the present case it may be due to the constriction of a membrane forming the outer layer of the chromatophore, which may perhaps be regarded as similar to a thin tonoplast bounding a vacuole. Progressive cleavage such as HARPER (21) has found in the sporangia of the fungi and slime molds, in which the mass of protoplasm is cut up by irregular cleavage furrows from the surface and from the interior, of course corresponds to the cell division and not to the division of the chromatophore in *Closterium*. The furrows in the sporangia are scattered throughout the cleaving mass, being perhaps due to an extrusion of water from its surface and interior, while in *Closterium* there is only one furrow, and this is localized in a definite zone at the middle of the cell. No nuclear changes are visible at this time, and any theories that connect nuclear division directly with cytoplasmic division, such as those of HEIDENHAIN and KOSTANECKI, would seem to break down in the present case.

The nucleus, in the meantime, has apparently undergone no change that is visible externally (figs. 1, 9), the granular mass at the center being still present. The nucleus is in the process of spireme and chromosome formation during the time the chromatophore is dividing, although this process is not visible externally. Soon, however, some individuals (fig. 2) show the chromosomes in the equatorial plate stage on a cylindrical spindle whose ends are hidden by the projecting chromatophores. The nucleus now apparently disappears (fig. 3); the chromosomes, being drawn back to the ends of the spindle, are under the ends of the chromatophore and cannot be seen. Across the middle of the cell there is now (fig. 3) a very conspicuous broad band of granular matter, in the middle of which the new wall is put across. The two nuclei, having been reconstructed, can then be seen moving out to the surface of the chromatophore and making their way back (fig. 4), immediately under the plasma membrane, to the new position they are to occupy permanently in the new cell at the middle of each chromatophore. FISCHER (14) states that these migrations

occur on both the concave and convex sides, but I have found them in these species to be practically all on the convex side.

The movement of the nuclei is apparently amoeboid, comparable to that of the male nucleus of the flowering plants in its progress toward the egg nucleus in the embryo sac. In the present case, however, it seems conceivable that the pushing outward of material into the new end of either daughter *Closterium*, combined with the change of shape which that end undergoes as soon as the new wall is formed, may assist to some extent in the movement of the nuclei. It will not explain it entirely, however, and we are forced to assume some stimulus that induces the nucleus to move to its new position. As long as the nucleus is at the end or along the side of the chromatophore, the two sides of the nucleus are exposed unequally to the food supply, and while the active streaming movements in the peripheral granular layer would partly equalize the deficiency, the side that is next the chromatophore is in touch with the soluble foods that are available there in greater quantity than at the side next the granular layer. The only way in which the nucleus can supply itself equally with food over its entire exterior surface is to imbed itself near the center of the chromatophore, and this is the position of course which it finally assumes. Other stimuli may of course also be in play.

Soon after the new cross-wall is put in at the middle of the desmid, the new end begins to round out, but the two organisms hang together for quite a time, with only a very slight connection (figs. 5, 6, 10). The connection finally breaks and the individuals separate before the new halves are at all symmetrical with the old ones (figs. 8, 12). The granular material which formed a band across the cell now makes a thin cap for each new half (fig. 6), the material in it being continuous with the plasma membrane and forming a conspicuous example of MOLL's embryonic substance. The change of form of this new end, resulting in an organism with symmetrical chromatophores, and the formation of the end vacuole in the granular portion follow slowly (figs. 8, 11, 12, 13). The process as we can see it, while superficially an apparently very simple one, is extremely difficult of explanation in terms of physics

and chemistry. It would seem to be necessary to assume some sense of form in the organism which MOLL has named "morphaesthesia," a striving of the individual to attain a certain shape characteristic for the species.

The apparently unequal division of the chromatophore attracted my attention, and in order to determine just what were the proportions of the dividing parts, I made

careful camera lucida drawings of six individuals of *C. Ehrenbergii* in early stages of division. It will be seen from the text figure, which is a composite one made from these six sketches, that the chromatophore division results in a cone and a frustum, and that apparently the cone is much the larger. The cubic contents of these two solids can be approximately determined, however, and the rather surprising fact is revealed that the cone has certainly not more than two-thirds the cubic contents of the frustum. It must be remembered, however, that the frustum end includes half of the large nucleus and of the vacuoles on either side of it which do not appear in the cone end. This blunt end is also the one which must undergo reconstruction, a process which undoubtedly uses up quite an amount of material

such as starch, of which this portion contains more than the cone. However, it is plain that it would be improper to speak of this new half as "growing out," in the sense that it has to grow in order to become as large as the pointed end. It contains at division as much, or probably more, material than the old end; there is a reshaping of this material, but both ends take part in the growth that is to produce again a normal size in the individual.



The nucleus in these two species seems to arrive regularly at the center of the new organism before the chromatophore has finished its division (figs. 5, 6, 8, 11). This confirms FISCHER'S (14) observation that the nucleus in *C. moniliferum* usually arrives at the constriction in the chromatophore before it is complete, and that the separation of the last strands is apparently finished under its direction.

The resting nucleus

As commonly figured in textbooks on the algae, such as OLT-MANN'S, the nucleus of *Closterium* is a lens-shaped or cylindrical body lying between the two halves of the chromatophore at the middle of the plant and containing a granular mass at its center. *C. moniliferum* is the species most frequently figured, and in it the drawings frequently show the two halves of the chromatophore pulled back from each other, with the nucleus lying as a cylindrical structure, somewhat contracted at the middle, connecting them.

I have already given a partial account (27) of the interesting and suggestive structure of the resting nucleus, but in connection with the present work I have of course carefully examined again great numbers of nuclei, both in whole mounts and in sections.

The nucleus is very large for an alga, and presents almost as favorable an object for study as does that body in the majority of the flowering plants. There is quite a little difference in its structure in the two species studied, although in a general way they are very similar, and are both essentially like that of *Spirogyra*. The nucleus of *C. Ehrenbergii* is in the form of a biconvex lens (figs. 14, 15), and I have never found it losing this shape as a result of the two halves of the chromatophore pulling away from each other. In end view it is circular in outline, as shown in fig. 16.

The mass of the nucleus is made up of a very fine reticulum which stains very faintly both in the triple stain and in the iron-hematoxylin, and shows a few such chromatin granules as occur on the linin threads of many of the higher plants. If such granules are present, they must be very minute or do not retain the stain. There are darker staining places in the reticulum, but I should be inclined to regard these as net-knots rather than as definite bodies. At the center of this fine reticulum is a mass of substance

which stains intensely with the safranin in the triple stain. This body, or mass of bodies, seems to be composed of globules partly fused together, and has the position and presumably the function of the nucleolus in other plant cells. In this species of *Closterium* these bodies form an irregular accumulation at the center of the reticulum, usually, at least partially, fused together in various ways, sometimes in the form of a string of beads stretched across the long axis of the cell, while at the other times the chain may be coiled around on itself, so that it simulates a spireme or has the appearance of the chromatin in the cells of the salivary gland of the *Chironomus* larvae. As would naturally result from the partial fusion of spherical granules, the individual pieces are angular on some of their sides, while rounded on others. It is not possible to determine whether, in the living cells, these globules are separate or not, or whether the partial fusion is due to fixation, such as sometimes happens in the case of chromosomes. Owing to the very faint stain which the reticulum takes and the very small size of its meshes, it is not possible to make out with any degree of certainty its relation to the central bodies.

In *C. moniliferum* (figs. 17, 18) the nucleus is composed, as in *C. Ehrenbergii*, of a very delicate reticulum containing apparently very little chromatin in the form of granules. At the center of this reticulum is usually found a large, more or less angular body, which apparently represents the irregular mass found in *C. Ehrenbergii* and the nucleolus of other plants. This nucleolus, while not having the smooth, homogeneous, globular appearance of that body in *Spirogyra*, still does not have the irregularly diffuse structure it presents in the other species of *Closterium* which I have studied. The pieces, while fused together, do not seem to form a compact mass. It has an irregular outline and shows lighter and darker places, if not stained too densely (fig. 17). The condition here would seem to represent an intermediate condition in the fusion of the nucleoli between that of *Spirogyra* and that of *C. Ehrenbergii*.

Prophase

As the formation of the spireme apparently requires a long time for its completion, the prophase is one of the stages that can be

found in great numbers. This is especially important for the question here involved, as it is one of the critical stages in which the relation of the compound nucleolus to the spireme and the chromosomes should appear.

As with mitosis in all plants, it is difficult to determine just the point at which the spireme starts to be differentiated out of the nuclear reticulum which gives rise to it. The reticulum seems to become drawn out into strands (fig. 19), but the exact method by which this takes place is not clear, for, as previously noted, the meshwork is a very delicate one, which stains very faintly and in which the structures are all very minute. These first strands, like the reticulum from which they are derived, apparently contain little chromatin in the form of granules (fig. 17), although a few such bodies are scattered in it; as the spireme grows more definite, however, there appear in it numerous small bodies which stain more densely (fig. 20).

The compound nucleolus, in the meantime, retains its position at the center of the nucleus, but the partly fused masses that composed it now becomes separated into small spheres that are independent of each other (figs. 19-23). This would seem to indicate that during the process of spireme formation, at least a portion of this central body is used. This body is suspended in the nuclear reticulum in some manner, but further than that it is not possible to see any connection between the two, such as has been shown for nucleoli in some animal cells, and by WAGER (45) in the nuclei of the root tip of *Phaseolus*, in which he states that the nucleolus is really only a very large granule or sphere on the linin thread. In the case of *Closterium* this central compound nucleolus apparently lies entirely clear of the reticulum, but this is undoubtedly only apparent, as it would not retain its central position in the nucleolus if it were not attached. If part of the material forming this body does pass out to assist in forming the spireme thread, the passage must occur while it is in a liquid state or as very small spheres. There is of course the possibility that the small, darker staining bodies on the spireme thread (fig. 20) may have migrated out in this manner, but the point to be particularly emphasized is that there is no passing out bodily of large pieces of this compound

nucleolus to form chromosomes on the spireme, as the compound appearance of that body in *C. Ehrenbergii* especially would indicate might happen. There seems to be no question that this body loses part of its material during the time of spireme formation, as its diminished size clearly shows, but it is no more possible here than it is in the flowering plants to prove directly that it is used to form the spireme. The spindle fibers are being formed at either pole, and it is entirely possible, as STRASBURGER believes, that it may be utilized in their formation. The apparently small quantity of chromatin in the reticulum, combined with the small size of the chromatin granules observed on it as compared with the density and size of the spireme, would certainly lead one to suspect, however, that the material from the diminishing nucleolus was being transferred to it. Of one fact there can be no question, and that is that the substratum of the spireme itself arises in the extra-nucleolar part of the nucleus, and not, as MITZEKEWITCH, BERGH, KARSTEN, and others have found in *Spirogyra*, inside the nucleolus, and that while the relation of the nucleolar material to this structure may not be clear, it does not seem to differ essentially from that which is found in the higher plants.

The spireme cuts transversely into chromosomes, no previous longitudinal split having been found, although it probably occurs. At the time this segmentation takes place, the spireme thread still has an irregular outline, due to small projections from its surface. These projections appear (fig. 24) also on the chromosome at first, but later disappear, and the chromosomes become long rods with a smooth surface.

In the meantime the ellipsoidal nucleus is undergoing changes in shape. Its smooth outline is lost and the nuclear walls are drawn out in places (figs. 19-21). The walls (fig. 24) are very much thickened at the future poles of the spindle, and a dense layer of fibers lies outside of them, while the equatorial walls are thin and irregular. Some of the figures obtained at this time resemble somewhat those of HERTWIG (24) for *Actinosphaerium*, although the thickening in the present case is not so great as is shown in his end plates. Some of these fibers extend out and are apparently attached farther back in the chromatophore, evidently serving

to attach the broad ends of the spindle, when it is fully formed and functioning, as a sort of anchorage for it. As a result of my observations I am of the opinion that the spindle itself is largely of cytoplasmic origin. The actual ingrowth of fibers which take hold of the chromosomes and later pull them apart was not observed. Strands of a lighter staining substance, probably what has been considered linin, connect the chromosomes to each other and to the nuclear wall (fig. 24). All that would seem to be necessary to form the attachment to the chromosomes would be a strengthening of those fibers extending to the nuclear wall. If this be true, there should be no fibers growing into the nucleus from the outside to take hold of the chromosomes, but only a thickening of those already present.

Metaphase

The spindle (fig. 25) is broad and as wide at the poles as at its middle. No bodies in the nature of centrosomes occur at the poles, which are broad and platelike structures (fig. 25) very similar to those described for *Spirogyra*. There are occasionally spherical bodies found in this region (figs. 28, 29), which may be metaplastic particles, or perhaps the remains of the old nucleolus, although this point was not worked out. The spindle is attached by fibers extending from it, especially at the two sides. It is not possible to determine just where the spindle ends (figs. 25, 26). In the equatorial plate are arranged the rodlike chromosomes (fig. 25). Attached to each chromosome are fibers from either pole which pull it into two parts by a longitudinal split (fig. 26). These fibers are in the figure attached toward the middle of the chromosome, although many were also observed in which the attachment was toward their ends.

Telophase

After the chromosomes have been pulled back to the poles (figs. 27, 28) in the usual manner, they lie there in the form of a plate which is more or less crescent-shaped in cross-section (figs. 29, 30). The broad central spindle remains connecting the two poles, but gradually disappears, taking no part in the formation of the new cell wall (fig. 30). The chromosomes at either pole

apparently unite end-to-end to form a dispireme (figs. 31, 32). The nucleus with the included spireme has originally the shape of the group of chromosomes in telophase, that is, a plate, and this is retained during the reconstruction stages. The spireme stains very densely at first (figs. 29-31) while it still retains all the chromatin, but later becomes so faint that it is difficult to see (fig. 32). The formation of the reticulum from the spireme cannot be followed with any great clearness on account of the small size of the parts. There is a reticulum formed (fig. 32) in some manner, however, and on it appear bodies which stain more densely than the meshwork by which they are surrounded. At first these bodies are small and numerous, but in the later stages (fig. 33) they have fused into masses of considerable size; these masses will later form the compound nucleolus. When the nucleus has been entirely reconstructed, these bodies still lie more or less scattered, and while the nucleus is making its way back to its new position (fig. 34) there are still usually at least two groups. Apparently it is only after it has come to rest at the middle of the daughter cell that all of these nucleolar bodies take their position at the center of the nucleus. The process, as will be seen from fig. 35, is essentially the same in *C. moniliferum* as in *C. Ehrenbergii* from which the other figures were drawn. In *C. Ehrenbergii* there is only a slight fusion in places, while in *C. moniliferum* it is sufficiently complete to make a fairly homogeneous structure.

After the nuclei have been reconstructed, they begin to move out to the surface of the cell (fig. 34) and then around the chromatophore. The chromatophore being evidently a very dense structure, it is apparently much easier to go around than to penetrate it. In *Spirogyra* the central part of the cell is almost entirely free from cytoplasm, and the daughter nuclei would meet no such obstruction. As previously noted, this migration occurs along the grooves of the chromatophore (fig. 7), where, as has been shown in my paper (27) on the chromatophore, there are fewer strands of cytoplasm to impede its passage.

As the nucleus in both species usually arrives at the new position some time before the chromatophore has finished its division, it is very common to find figures like nos. 6, 8, 11, and 36, in which

the final separation of the two halves seems to occur "under its direction." In sections, the relation of the plasma membrane to the vacuole which is cutting the chromatophore in two is brought out very clearly (fig. 36).

It is not possible to learn more of the movement of these nuclei in sections than it is in whole mounts. The process, however, seems to be some kind of an amoeboid one, judging from the changes in shape the nuclei undergo in the process.

The formation of the daughter cell walls

There seems to be a general agreement that in the Conjugatae the new cell wall arises by a growth inward from the old wall, in which the spindle fibers, unlike those of higher plants in which a cell plate is formed, take no part. The central spindle remains in place while the wall is growing (figs. 27, 29), but seems to take no visibly active part in its formation, although there is the probability that its material may be used up to form the new plasma membrane. It is to be noted further that none of the fibers of the central spindle persist (figs. 33, 34) until they are cut in two by the ingrowth of the wall from the sides, as occurs in *Spirogyra*.

The process of new wall-formation is essentially the same in the two species of *Closterium* studied as in *Spirogyra*. After the chromosomes have been drawn back to the two poles, the large central spindle, which previously had been very conspicuous, disappears, and in the later stages of the telophase all that can be seen of it are a number of fibers extending through the region it formerly occupied (fig. 29). The cross-wall begins to grow in during metaphase, the process starting at the periphery of the cell and seeming to be due to constriction of the plasma membrane. Preceding and also accompanying this growth of the plasma membrane a layer of granular cytoplasm appears, in which the streaming movements are very noticeable in the living specimens. The new wall cuts across the spindle fairly at its center, being a third of the way across by the time the fibers have disappeared. Connecting the two nuclei is a granular band which, connecting with the ingrowing plasma membrane, gives the appearance shown in fig. 3 to the external view of the whole mount. By the time the

nuclei are entirely reconstructed, the new wall is about two-thirds of the way across in section, and the nuclei move out to the surface of the chromatophore and are making their way back to their new position before the remaining part is closed (fig. 34). It would seem from this that the presence of the two nuclei is not required for the completion of the cell division, but that the material for the new wall is there and the process is well begun before they begin their migration. It will be particularly noted that the new wall is put in at right angles to the old side walls.

It is clear that the younger end of the new individual will be covered partly by the new transverse wall that is becoming pushed out into a cone (figs. 11-13) and partly by a portion of the old parent cell wall. Where these two portions meet, the so-called girdle band appears in certain species, but in the two forms under consideration it is soon difficult to distinguish the point of union of the old and new walls, although it can be seen in individuals recently divided (fig. 8).

General considerations

FISCHER (14) has already pointed out the fact that it is due to the method of origin of the daughter chromatophores by division that the ridges of the chromatophore on either side of the nucleus correspond, as each ridge was cut in two when the chromatophore divided. It is to be further noted that the division of the chromatophore also explains the continuity of the outer granular layer, in which the streaming occurs, across the region separating the two halves of the chromatophore. When the chromatophore is pinched into two parts, the constriction process takes place inside this granular layer, which is not divided, but is left intact to form the outer wall of the ring-shaped vacuole. In *Closterium*, as seen during the daytime, this granular membrane is still continuous, and in it occurs the very active streaming movement between the two parts of the chromatophore.

The time relation between the division of chromatophore and nucleus in these plants is an interesting one. *Closterium* as seen in the daytime has its chromatophore divided into halves. These two halves are the result of the chromatophore division of the

preceding night. In these species of *Closterium*, however, they are further to be looked upon as being a preparation for a division of the nucleus and cell the following night, providing it has been successful in storing enough food material to make the process possible. If the individual is not able to synthesize enough starch, the nuclear and cell division is not carried out, and the two-parted chromatophore is retained indefinitely. In these species of *Closterium*, cell and nuclear division is at least a two-night process: the first night the chromatophore divides, cutting in two the greater part of the cytoplasm, but still retaining a connection between the two parts by means of the granular peripheral layer; the second night the nucleus may divide and the new wall separate the cytoplasmic halves entirely by cutting through the granular layer.

The question of the relation of the nucleolus to the chromatin, especially in the division stages of that part of the nucleus, is still an unsettled one both for plants and animals, and it is one that comes sharply into the foreground in this study of the division of the nucleus of *Closterium*. It would seem probable that, if the globular and nearly homogeneous nucleolus of *Spirogyra* contains the entire mass of chromatin in the form of a condensed spireme thread, as MOLL (32), MITZKEWITCH (31), KARSTEN (25), and others have found, this much more strikingly compound nucleolus of *Closterium*, arranged occasionally so as to resemble a spireme, should represent the chromosomes aggregated into a central clump. That the chromosomes are really formed from the nuclear reticulum in *Closterium* is certainly very decisive as to their morphological independence. The spireme formed outside the compound nucleolus seems indeed to be poor in chromatin, and the probability of the nucleolar material being used in the formation of the spireme cannot be denied. This, however, is also in some degree the case in the nuclei of the higher plants, and we are bound to conclude that the relations of nucleolus and chromosomes are probably the same in all nuclei, in spite of the much discussed evidence for a chromatin nucleolus in the Conjugatae.

If the spireme really thickens by the absorption of liquid material derived from the nucleolus, this can hardly be regarded,

as WAGER (45) holds, as evidence for the idioplasmic nature of the latter. The growth of the chromosomes from one cell generation to the next is still too obscure a subject to permit the use of such an interpretation.

As noted above, STRASBURGER (40), as a result of his work on *Marsilia*, in which he found the nuclear reticulum very poor in chromatin while the nucleolus was very large, holds the view that the linin may be the bearer of hereditary qualities, while the chromatin is only a food substance which divides simultaneously. This hypothesis is of interest, and it may be admitted that the recent attempts of BOVERI (4), ROSENBERG (36), OVERTON (34), and others to show that the chromosomes are permanent organs of the cell may be interpreted in support of the theory that the linin substratum of the chromosome is its more essential constituent, while the visible and more conspicuous chromatin granules only serve as conveniently scattered food.

Of interest also in this connection is the recent attempt of GRÉGOIRE (20) to show that the nuclear reticulum is all one substance, with no differentiation into chromatin and linin. These two species of *Closterium*, and in fact the Conjugatae in general, might be regarded as having a nuclear reticulum composed of a single substance; still they are perhaps not the most favorable material on which to study this question.

The chromosomes do not come bodily out of the nucleolus of *Closterium*, but that structure disappears during the prophase as in other cells, and we have as yet only theories as to its fate. In the present case the theory based on the observations of MOLL (32), MITZKEWITCH (31), KARSTEN (25), BERGH (2), and others, that as in *Spirogyra* the chromosomes are included morphologically complete in the nucleolus, would not be of service in these species of *Closterium*. In like manner the observations of VAN WISSELINGH (43) on *Spirogyra* and of Miss MERRIMAN (29) on *Zygnema*, that a number of the chromosomes come out of the nucleolus, would not apply in the present case. While the evidence in *Closterium* is not at all complete, the conclusion reached by ESCOYEZ (12, 13) on *Zygnema* and *Stypocaulon* would seem to be most in line with my own observations. These are, that while

the chromosomes do not come morphologically from the nucleolus, there is a possibility that part of the material from that body goes to form them.

The relationships of the desmids to the other groups of the Conjugatae is a rather puzzling one. While the great majority of them are unicellular, the tendency to form filaments appears in such genera as *Cosmarium*, *Euastrum*, and *Staurastrum*. BESSEY (3) has gone so far as to divide the desmids on this basis into three tribes: Desmideae, cells in unbranched filaments: Anthrodieae, cells solitary, elongated, but at not all or only moderately constricted; Cosmarieae, cells solitary, broad, and deeply constricted.

WEST (46) in studying variation in desmids came to the conclusion that the group is a degenerate one derived from a filamentous conjugate ancestor, probably among the Zygnemaceae. On this basis of degeneration he claims to be able to explain many facts previously difficult of interpretation. He holds that this degeneration has developed the highly specialized morphological characters of the different groups, thus explaining their beauty and variety of form, and that with it too has gone hand in hand the loss of sexual differentiation of the conjugating cells. LÜTKEMÜLLER (26), as a result of his very careful study of the cell wall of members of the different groups of desmids, has arrived at practically identical conclusions as to their phylogeny.

The position of the young transverse wall in *Closterium* also seems to throw some light on this question of phylogeny. The new cross-wall is put in at right angles to the old walls in a manner that is not in any essential different from that of the filamentous Conjugatae such as *Spirogyra*. It is only as the cells separate and the pressure is relieved on one side of this wall that the shape changes. If the cells should not separate, a filament being formed, each cell of the filament would not be essentially different from a cell of *Zygnema* with its nucleus at the middle and a half of the symmetrical chromatophore on either side. While the pointed shape which the new end assumes is obviously a secondary and acquired character, in the ontogeny of the transverse wall, we would seem to have a bit of the phylogeny of *Closterium* repeated.

Summary

1. *Closterium* divides from 10 P.M. to 5 A.M., and the new half has become practically symmetrical with the old one by 9 A.M.
2. Division is dependent upon the storage of a considerable quantity of starch in the chromatophore and around the pyrenoids.
3. The chromatophore divides by a constriction located about a third of the distance out from the middle. This constriction is due to the enlargement of a ring-shaped vacuole under the plasma membrane.
4. The resting nucleus of *C. Ehrenbergii* is made up of a very fine reticulum carrying little if any chromatin in the form of granules. At the center of this reticulum is a large compound nucleolus made up of a number of partially fused nucleoli. The resting nucleus of *C. moniliferum* has essentially the same structure, but the nucleoli at the center are more completely fused.
5. The spireme is formed outside the nucleolus and apparently separate from it. During its formation that body breaks down, but it is impossible to decide whether its material goes to the spireme or is used up for some other purpose. No chromosomes come bodily out of the nucleolus as has been described for *Spirogyra*.
6. The spindle is cylindrical, with broad poles, much resembling that of *Spirogyra*.
7. In the telophase a dispireme is formed, and in this the nucleoli reappear as small spheres which later partially fuse to form larger masses.
8. The two daughter nuclei move around the chromatophore, between its ridges, apparently in an amoeboid manner, to their new positions.
9. The new end wall is put across in essentially the same manner as in *Spirogyra*, that is, by a growth inward from the periphery.
10. Division in these species of *Closterium* is at least a two-night process: the chromatophore divides the first night; the nucleus the second night.
11. The position of the young transverse wall would seem to indicate that the pointed ends are secondarily formed, and that *Closterium* was originally a filamentous alga, which has developed the habit of breaking up into single cells.

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EXPLANATION OF PLATES XXII AND XXIII

All figures were drawn with the aid of a camera lucida; the majority of them with the Leitz $\frac{1}{8}$ achromatic objectives and eyepieces, and the others with the Zeiss 3 mm. apochromatics and compensating oculars. The approximate magnification is indicated after each figure. Figs. 1-13 are from whole mounts in glycerin, and are diagrammatic in that they do not show the slight shrinkage of cell contents due to fixation and transfer to glycerin. The other figures are all from sections 5-10 μ in thickness, stained with the triple stain, except fig. 29, which is from a slide stained with iron-hematoxylin.

C. Ehrenbergii

- FIG. 1.—Chromatophore just beginning to show constrictions; $\times 300$.
- FIG. 2.—Nucleus in metaphase; transverse cell wall beginning; $\times 300$.
- FIG. 3.—Transverse cell wall nearly complete; nuclei not showing; $\times 300$.
- FIG. 4.—Transverse wall complete; nuclei moving back to their new position; $\times 300$.
- FIG. 5.—New ends beginning to round off; nuclei at constriction; $\times 300$.
- FIG. 6.—New end still further rounded; $\times 300$.
- FIG. 7.—Position of nucleus between the ridges of the chromatophore as seen from the convex side; $\times 300$.
- FIG. 8.—Individual with asymmetrical halves; the chromatophore not yet completely divided; the new tip beginning to assume its pointed shape; $\times 300$.

C. moniliferum

- FIG. 9.—First appearance of constriction in the chromatophore; pyrenoids dividing; $\times 550$.
- FIG. 10.—Individual with two halves just ready to separate; $\times 550$.
- FIGS. 11-13.—Various stages in the change of form of the new halves; fig. 11 showing pyrenoids dividing; fig. 11, $\times 550$; figs. 12, 13, $\times 475$.

C. Ehrenbergii

- FIGS. 14, 15.—The resting nucleus in side view; $\times 1800$.
- FIG. 16.—Resting nucleus in end view; $\times 1800$.

C. moniliferum

FIG. 17.—Resting nucleus in side view; $\times 1800$.

FIG. 18.—Resting nucleus in end view; $\times 1800$.

C. Ehrenbergii

FIG. 19.—First traces of spireme formation; $\times 1800$.

FIGS. 20, 21.—Later stages of spireme; $\times 1800$.

FIG. 22.—Detail spireme showing chromatin granules; $\times 1800$.

C. moniliferum

FIG. 23.—Spireme; nucleolus breaking up; $\times 1800$.

C. Ehrenbergii

FIG. 24.—Chromosomes formed; $\times 1050$.

FIG. 25.—Metaphase; $\times 1050$.

FIG. 26.—Detail of metaphase; $\times 2400$.

FIG. 27.—Anaphase; $\times 1050$.

FIG. 28.—Late anaphase; $\times 1800$.

FIG. 29.—Telophase: spindle fibers still showing; $\times 1050$.

FIG. 30.—Telophase; spindle fibers have all disappeared; wall touching remains of central spindle; $\times 1050$.

FIGS. 31, 32.—Telophase; dispireme; nucleoli reappearing in fig. 32; $\times 2400$.

FIG. 33.—Late telophase; nucleoli fusing to form large masses; $\times 1050$.

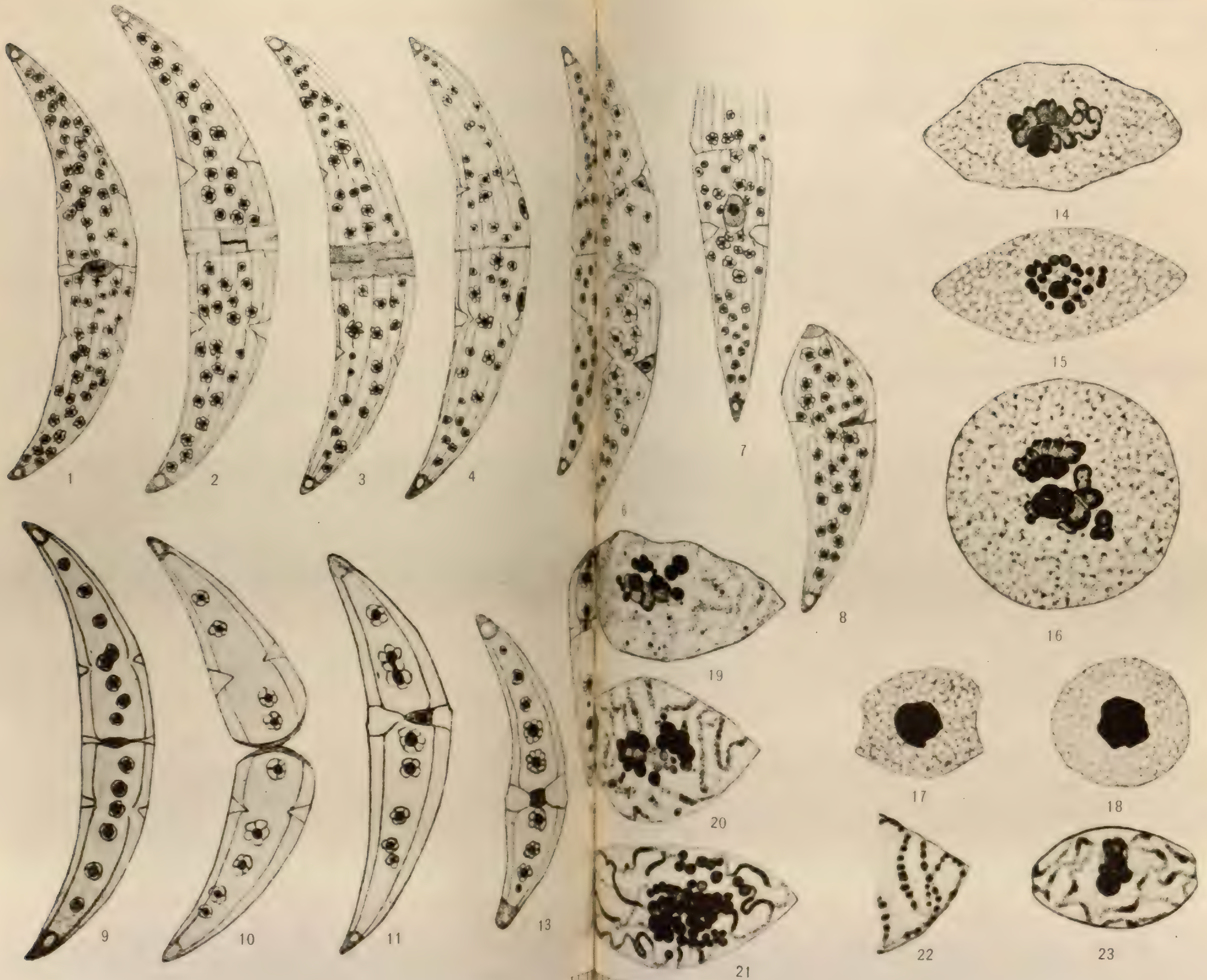
FIG. 34.—Nuclei moving out to surface of chromatophore; both nuclei still showing a number of masses of nucleolar material; cell wall not yet completed; $\times 1050$.

C. moniliferum

FIG. 35.—Late telophase; nuclei reconstructed, but nucleoli not yet fused to form a single mass; cell wall beginning; $\times 1050$.

C. Ehrenbergii

FIG. 36.—Nucleus in its new position at constriction in chromatophore, but latter not yet divided; *pp*, granular layer; $\times 1050$.





LUTNERIUM

THE GENUS EVERNIA AS REPRESENTED IN NORTH AND MIDDLE AMERICA

R. HEBER HOWE, JR.

(WITH PLATES XXIV AND XXV)

Genus: EVERNIA Ach. Lich. Univ. 84 et 441. 1810

The species of the genus, since 1753, have appeared under the following: *Lichen* L. (1793), *Lichenoides* Hoffm. (1790), *Lobaria* Hoffm. (1795), *Usnea* Hoffm. (1795), *Parmelia* Ach. (1810), *Borrera* Ach. (1810), *Physcia* DC. (1815), *Cornicularia* DC. (1815), *Ramalina* Chev. (1826), *Archevernia* Th. Fr. (1831), *Letharia* Th. Fr. (1831), *Phacopsis* Tul. (1852), *Chlorea* Nyl. (1859), *Rhytidocaulon* Nyl. (1859), *Alectoria* Mudd (1861), *Nylanderaria* Kuntze (1891); comparatively few of these, however, are generic synonyms.

DESCRIPTION: *Apothecia* subterminal, marginal or lateral; scutelliform, applanate or concave, sometimes convex and lacerate; marginate (thalloid dilations=*vulpina*); thalline exciple *rugose*; disk chestnut. *Asci* clavate, containing eight spores; paraphyses gelatino-filamentous. *Spores* monoblast, hyaline, ellipsoid. *Spermatogones* immersed, black. *Sterigmata* branched, articulate. *Spermatia* acicular, incrassate near apices.

Thallus caespitose, subpendulous or pendulous, branched; cortex *rugose*, sometimes perforate, smooth, furfuraceous or isidioid, subterete (subradial), compressed (bifacial) or angulate; rhizinae rarely present; sulphur yellow, stramineous, virescent-stramineous, or cinereous; *medulla* cottonous, arachnoid, or somewhat coalescent. *Gonidia*, *Protococcus* (*Cystococcus humicola* Naeg.). *Soredia* normal. *Cephalodia* small, often warty, concolorous, sea-green or black, often gelatinous.

OBSERVATIONS: After all has been said, I can see no sufficient reason for separating the genus as given by TUCKERMAN. That the species here considered all have *cottonous* arachnoid medullas, whether more or less coalescent, cannot be questioned, and in none of the species does a true *chondroid*, axial cord exist. This slight variation in the condition of the medulla (one more or less of growth) does not in the least justify generic separation. It is true, as TUCKERMAN pointed out, that thalline differences must always constitute our criteria for generic distinction in this most difficult group of plants; yet if

thalline differences are recognized beyond a certain plausible degree, it is hardly exaggerating to say we shall have eventually nearly as many genera as species. In fact in the present genus this is now almost true. In true *Evernia prunastri*, the type of the genus, a bifacial structure of the laciniae is evident. This condition becomes obscure in the variety *thamnodes*, and in *vulpina* it is nearly radial. In *divaricata* the bifacial structure is about as in *thamnodes*, while in *Trulla* and true *furfuracea* it is markedly bifacial (*parmelioid*), but in the latter's varieties (apical portions) *ceratea* and *cladonia* the radial structure is again approached. If a careful study of the thalline structure of the species here considered is made, it will be seen that the pendulous, prostrate condition of growth typical of this genus tends to destroy a complete radial development. A portion of some of the branches of almost every individual plant shows a bifacial structure, owing to the gonidia seeking the uppermost or light-exposed side. In the truly pendulous *Usneas* and *Alectorias*, and wide branching, rigid, non-prostrate *Ramalinas*, and in the rigid caespitose species of the two former genera, the complete exposure develops a truly radial structure. In the present genus, it is not strange therefore that we find the luxuriant and more rigid examples of *vulpina* and the longest pendulous specimens of *divaricata* most nearly approaching the radial condition. In other words, so far as the sectional structure of the laciniae is concerned, *Evernia* holds an intermediate position between the strictly radial *Usneae* and *Alectoriae*, and the bifacial *Parmeliacei*.

The rare tropical lichen *Evernia Trulla* (Ach.) Mont. was set apart by NYLANDER in a unique genus, *Everniopsis*. I have been able to study but one specimen of this plant, kindly loaned me by the National Museum, and the scarcity of material thus precludes a sufficient study to settle satisfactorily the question of its classification in my own mind. There is no question that the plant morphologically is nearest to *furfuracea*, as TUCKERMAN pointed out, and its bifacial and membranaceous thallus can hardly be said to have a chondroid axis, in fact a compressed stuppeous condition is all that appears to me evident.

The striking similarity between the corniculate smooth *Evernia furfuracea* var. *ceratea* (Ach.) Nyl. from the highest alpine zone, and *Parmelia physodes* var. *vittata* Ach. is undebatable, and extends somewhat further than a mere superficial resemblance. In fact, the points of differentiation are hardly traceable, lying for the most part in the inflated laciniae, and ecanaliculate condition of the thallus. This striking similarity attracted the attention of NYLANDER and CROMBIE, and was perhaps the cause of the glossarial adjective "evernioid."¹ There is every reason to hold this genus in close proximity to *Parmelia*.² *Evernia* (? *Alectoria*, *Letharia*) *canariensis* (Ach.) Nyl. shows also

¹ NYLANDER, *Flora* 52:445-446. 1869.

² *Parmelia Camtschadalis* var. *americana* (Mey. et Flot.) Nyl., except for its rhizinae, strongly resembles this variety, a canaliculate condition being here present.

its close relation to *Alectoria*, as *Evernia trulla* (Ach.) Mont. likewise suggests a *Cetrarian* relationship, through *Platysma everniellum* Nyl., etc. Dr. ZAHLBRUCKNER has placed *furfuracea* with the *Parmelias*, but has left *prunastri* with this genus. To me this seems inconsistent, as both are structurally bifacial,³ though the former rarely shows a few rhizinae. He has also included *divaricata* under his *Letharia*, separating it thus generically from *prunastri*.

From the foregoing observations it is evident that this complex genus presents a transitional thalline condition, which though undeserving separation, as already pointed out, will be made more clear perhaps, if three sectional distinctions are indicated in our nomenclature. This was done in part by TH. FRIES in 1871.

Section: LETHARIA Th. Fr. Lich. Scand. 32. 1871

Thallus subradial, medulla cottonous, coalescent into axial strands

EVERNIA VULPINA (L.) Ach.

TYPE: Not indicated; the specimen on which LINNAEUS based his species is in the Dillenian herbarium, Botanic Gardens, Oxford, England, and according to CROMBIE and earlier writers is "*Physcia flavicans* (Sw.)" = *T[h]eloschistes chrysophthalmus* var. *flavicans* (Ach.) Tuck. All the pre-Linnaean botanists referred to the same Dillenian plate and specimen, and were followed by LINNAEUS. VILLARS in 1789, however, described diagnostically the true *Evernia* from Briançon, France, basing his species on HALLEY, who questioned his own reference to the Dillenian plate. SOWERBY, E. FRIES, and other authors previous to 1831 were aware of the Linnaean misconception. FRIES, however, followed ACHARIUS, as have all since, saluting the *Evernia* by the name *vulpina*. As the "Ulf-Mossa," however, according to NYLANDER, is a common plant in Scandinavia, and *flavicans* not only is not listed but is an austral species, it seems probable that LINNAEUS gave the name to the proper plant, and his reference to the *Teloschistes* was an error. WAINIO also states that in the Linnaean herbarium "78 *Lichen vulpinus* = *Evernia vulpina* Ach."⁴ The substrate given for *vulpina* by LINNAEUS is certainly more characteristic of the *Evernia* than of *flavicans*, i.e., "tectis, ligneis, muris." The name *vulpina* has stood now for nearly two centuries, and on account of the Linnaean error it would seem inadvisable to drop it for *aurata* of VILLARS,⁵

³ "*Facie dissimilis*," HUE, Nouv. Arch. Hist. Nat. 8:(4) 119. 1899; "dorsiventral," ZAHLBRUCKNER, Nat. Pflanz. 217. 1907.

⁴ Meddel. Soc. pro Fauna et Flora fennica 14:10. 1886.

⁵ Professor MIRANDE, Université de Grenoble in litt. states that VILLARS' type is not now in the remains of his herbarium in the Museum of the Ville de Grenoble; see NYLANDER, Bull. Bot. Soc. France 10:954. 1863.

the next available name; the type of which, according to NYLANDER, was in existence in 1863; according to Professor MIRANDE, under date of February 8, 1910, is not now to be found at Grenoble.

TYPE LOCALITY: "Europae."

ORIGINAL DESCRIPTION: "filamentosus ramosissimus erectus fastigiatus inaequali-angulosus."

FIGURE: SCHNEIDER, Guide to Lich., 2 ed. *pl.* 4. 1904.

SYNONYMY: *Lichen vulpinus* Linn. Spec. Pl. 2:1155. 1753; *Evernia vulpina* Ach. Lich. Univ. 443. 1810.

DIAGNOSIS: *Thallus* loosely caespitose, subterete, rugose, sulphur-yellow.

DESCRIPTION: typical. *Thallus* loosely caespitose, subterete to compressed (rarely pendulous), rigid; cortex rugose-lacunose, rarely perforate, sometimes proximally expanded and glabrous; virescent to sulphur-yellow; *primary branches* coarse, dichotomous, divaricate (max. length 15 cm.); *secondary branches* dichotomous, divaricate and attenuate. *Apothecia* subterminal, ample (max. diameter 2.6 cm.), appendiculate, thalline exciple rugose and expanding, disk chestnut, emarginate and ciliate. *Spores* 5-8.5 $\times$ 4.5-5.5 μ .

CONTINGENT PHASES: (a) thallus spotted with minute black dots (spermogones), finally largely blackening; (b) reduced, sterile and virescent; (c) yellow soresiate (*E. v. γ incompta* Ach. Lich. Univ. 444. 1810).

SUBSTRATA: Trees, fences, and occasionally on rocks (limestone).

GEOGRAPHICAL DISTRIBUTION: Common in the lower Boreal zone, reaching rarely the Transition. The species extends from the mountains of Lower California, 8500 ft. (*Hasse*), and Mexico, Orizaba Mt., 9000 ft. (*Stone*), northward to British Columbia (*Macoun, Herden*) and Alberta (*Macoun* and others). It occurs up to 10,000 ft. in the Rocky Mountains. Though not included in Miss G. E. COOLEY's list of "Plants collected in Alaska and Nanaimo, B.C.," etc., nor in Miss CUMMINGS' "The lichens of Alaska," though she determined Miss COOLEY's plants, yet in the Herbarium of the New York Botanic Gardens there are two sterile examples labelled *vulpina* in Miss CUMMINGS' handwriting, on a "Flora of Alaska" label "collected by Miss GRACE E. COOLEY." Although Miss COOLEY did not include the species in her list at all (from either Alaska or B.C.), yet it is most probable that the above specimens came from the latter place. Eastward this plant extends to Montana (*Rydberg, Vreeland, Williams*), Wyoming (*Willey*), Black Hills, South Dakota (*Hayden*), Nebraska (*Fink*), and Grant Co., Nebraska (*Rydberg*), from where I have seen it fertile. It is reported also from Wisconsin or

Minnesota (*Parry*) by Professor FINK.⁶ It is rarely found fruited, however, near the geographical and altitudinal limits of its range.

OBSERVATIONS: This species owing to its vivid color is the most conspicuous of the genus. Though a new generic name (*Chlorea*) was proposed by NYLANDER for this and a few other species, and earlier a title *Letharia* (see WAINIO) by Th. FRIES (later again *Nylanderaria* Kuntze), as before stated there is no good reason for this distinction. A study of the plant shows intergrades approaching *prunastri*, through its variety, in thalline structure (and color), and it is quite evident that morphologically this species differs from *prunastri* less than *furfuracea*, with which *prunastri* has stood since 1825. The robust plant growing in the regions of heavy rainfall in California, Washington, and Oregon (set apart as var. *californica* by NYLANDER, though named already by NUTTALL⁷ *columbiana* in 1834, if not by ACHARIUS *xantholina* in 1810), is not in the author's opinion worthy of varietal rank.

Section: ARCHEVERNIA Th. Fr. Lich. Scand. 29. 1871

Thallus bifacial to subbifacial, medulla cottonous

EVERNIA PRUNASTRI (L.) Ach.

TYPE: Not indicated; one of the specimens on which LINNAEUS based his species is in the Dillenian herbarium, Botanic Gardens, Oxford, England, and according to CROMBIE is "sterile." According to WAINIO "39 *Lichen prunastri* = *Evernia prunastri* Ach." as represented in the Linnaean herbarium.

TYPE LOCALITY: "Europae."

ORIGINAL DESCRIPTION: "foliaceus erectiusculus lacunosus: subtus tomentosus albus." Linn. Spec. Pl. 2:1147. 1753.

FIGURE: [DILL., Hist. Musc. pl. 21. f. 54 = *E. p.* var. *gracilis* Ach.; 55a = *E. prunastri* (L.) (*soredifera*); c and d = *E. prunastri*, Ach.; h = *E. p.* f. *retusa* Ach. fide CROMBIE].⁸

SYNONYMY: *Lichen prunastri* Linn. *ibid.*; *Evernia prunastri* Ach. Lich. Univ. 442. 1810.

DIAGNOSIS: *Thallus caespitose* or subpendulous, *compressed* (bifacial), *rough*, *sorediate*, virescenti-stramineous.

DESCRIPTION: typical. *Thallus* loosely caespitose, subpendulous or pendulous, mollitinous, compressed, at length expanded, channeled, and paler below; *cortex* rugose-lacunose, more or less sorediate, stramineous to virescent; *primary branches* coarse,

⁶ It is recorded from Maine (ECKFELDT, J. W., Flora Mt. Desert, Me., 252. 1894), but the record is very doubtful and needs verification. The record probably refers to the var. *thamnoides*.

⁷ Jour. Acad. Nat. Sci. Phila. 7:59. 1834.

⁸ Pre-Linnaean references in brackets.

dichotomous, divaricate (max. length 12 cm.); *secondary branches* dichotomous, divaricate, furcate. *Apothecia* lateral, subpedicellate (max. diameter 6 mm.), disk chestnut, emarginate. *Spores* 5-7 $\times$ 3.5-4.5 μ .

CONTINGENT PHASES: (a) more or less completely sorediate (*E. p. soredifera* Ach. Lich. Univ. 443. 1810).

SUBSTRATA: Trees, dead wood, fences, roofs, and occasionally on rocks.

GEOGRAPHICAL DISTRIBUTION: This species is confined in North America to the Pacific coast. I have examined specimens from the San Gabriel Mts., Cal., northward to British Columbia. Its variety is the plant found throughout the rest of our area.

OBSERVATIONS: This lichen with its variety shows a common tendency (see *Usnea*) to vary from virescent on the Atlantic coast to stramineous on the Pacific. Specimens from the southwest have an inclination to expand their laciniae and to become channeled below, suggesting *furfuracea*. The apices are also more truncate and furcate; in fact the plants are comparable with the temperate European specimens which represent true *prunastri*; but both in Europe and throughout our area intergradation is shown, diverging types of laciniae occurring rarely in a single plant. Specimens from east of the Rocky Mountains and from Alaska are of the linear type, and were referred by WILLEY to *E. thamnodes* Nyl.⁹ To settle upon the rightful name for this linear plant is most perplexing. It appears, however, as follows: The oldest traceable name that has been used is *arenaria* Retz., but the type of *Lichen arenarius* Retz.¹⁰ has been kindly sent me by Professor OTTO R. HOLMBERG of Lund, and proves to be *Evernia divaricata* (L.) Ach. as cited by ACHARIUS, and not as by FRIES and NYLANDER as a variety under *E. prunastri*. The next possible cognomen used was given by ACHARIUS γ *gracilis* (l.c. 442), with the locality "Sveciac." In his herbarium, however, WAINIO¹¹ cites two specimens, one from "Helvetia" and one from "Kamtschatka." The former he says has "laciniis laevissimis" and seems a young form of *prunastri*, to which, he writes, ACHARIUS' second description (*Obs.*) without doubt refers. The latter specimen he says intermixed with it is *E. mesomorpha* Nyl. In the Acharian herbarium today (*fide* ELFVING) only the Kamtschatka specimens exist. Seeing therefore that ACHARIUS in his original description used the words "laciniis laevissimis"; that the Swedish plant has not been found in the herbarium; and that the one specimen, apparently lost, was "laevissimis," a character in no way fitting our variety, we must pass on to the next available name. This we find was given by FLOTOW (l.c.) in a very

⁹ FLOTOW, Lich. Schles. no. 54 c. 1829; and KOERBER, Syst. Lich. Germ. 42. 1855.

¹⁰ Fl. Scand. Ed. 2. 292. 1795.

¹¹ Meddel. Soc. Faun. et Fl. 8:117. 1881.

rare text accompanying his exsiccati which I have been unable to see, but is later cited by KOERBER as a trinomial: *Evernia prunastri* β *thamnodes* Flot. KOERBER curiously enough makes it synonymous with *Physcia divaricata* β *arenaria* Schaerer, showing the cycle of error caused by the RETZIUS specimen. HUE has used this name for our plant in the combination *Letharia thamnodes* (l.c. 58). NYLANDER described *E. mesomorpha* (Lich. Scand. 74. 1861), a name now generally considered synonymous; and again in the last year G. K. MERRILL distributed the plant as *Evernia prunastri* form *mollis* Merrill (Lich. exs. no. 51). It is very unlikely that the var. *vulgaris* Koerber (l.c.) is a synonym of *thamnodes*, but it seems quite plain that *gracilis* Ach. and *stictoceras* Sowerby are synonymous and do not refer to this plant; and it is not improbable that *E. mesomorpha* f. *esorediosa* Nyl. (Lich. Japan. 25. 1890) belongs with these.

EVERNIA PRUNASTRI var. THAMNODES Flot.

TYPE: No. 54c FLOTOW, Lich. vorzüglich in Schlesien 1:1829.

TYPE LOCALITY: "Sveciae."

ORIGINAL DESCRIPTION: "Thallus utrinque concolor laciniis longioribus angustioribus implexis verrucoso-furfuraceis" (KOERBER); and "Fruticulosa, undique corticata, similis verrucoso-furfuracea" (WENDT, Thermen zu Warmbrunn, 94. 1840).

FIGURE: HOWE, Common and Conspicuous Lich. N.E. pt. 1. 24. 1906. FINK, Lich. Minn. Cont. U.S. Nat. Herb. 14: pl. 39. 1910.

SYNONYMY: *Evernia prunastri* β *thamnodes* Flot., KOERBER, Syst. Lich. Germ. 42. 1855.

DIAGNOSIS: *Thallus* prostrate, *subterete* (subradial), rough, *virescent*.

DESCRIPTION: typical. *Thallus* caespitose, prostrate, subterete; *cortex* rugose, rarely soresiate, virescent; apices of branches *acuminate*; otherwise as in last.

SUBSTRATA: Same as last.

GEOGRAPHICAL DISTRIBUTION: Found throughout the Transition and lower Boreal zone. It is reported from Newfoundland (*Eckfeldt*) and from Manitoba (*Macoun*) and Vermillion Lake, Ontario (*Arthur*, etc.). It becomes rare, however, in northern Maine and Oregon, and is not reported from Labrador. RICHARDSON collected it, however, in Arctic America, Ft. Franklin, Great Bear Lake (1836), and I have examined several fertile specimens collected on *Betula* at Dawson, Yukon, Canada, by Mr. R. S. WILLIAMS early in the spring of 1899. HUE records *E. thamnodes* (Flot.) Nyl. from Port Clarence, Alaska, the White Mts., and "Ottawa." Southward it extends to the border of the upper Austral zone. I have seen specimens from New York (*Harris*, *Blake*), Fayette, Iowa, Minnesota, Ohio, and Nebraska (*Fink*). SWARTZ recorded it (?) from the West Indies (1791).

It is this variety that has been commonly distributed as *Evernia prunastri* in most of the North American exsiccati.

EVERNIA DIVARICATA (L.) Ach.

TYPE: Not indicated; the specimen on which LINNAEUS based his species is in the Dillenian herbarium, Botanic Gardens, Oxford, England, and "is represented . . . by only two or three sterile laciniae" according to CROMBIE. According to WAINIO, "*Lichen divaricatus* = *Evernia divaricata* Ach.," as represented in the Linnaean herbarium.

TYPE LOCALITY: "Helvetiae."

ORIGINAL DESCRIPTION: "filamentosus pendulus angulatus articulatus intus tomentosus, ramis divaricatis, peltis orbiculatis sessilibus." Linn. Syst. Nat. 713. 1767.

FIGURE: [DILL., Hist. Musc. *pl.* 12. *f.* 5. 1741]. HOFFM., Descript. et adnum. Lich. *pl.* 67. *f.* 1, 2, 3. 1801.

SYNONYMY: *Lichen divaricatus* Linn. Syst. Nat. *ibid.*; *Evernia divaricata* Ach. Lich. Univ. 441. 1810.

DIAGNOSIS: *Thallus* pendulous, *flaccid*, *compressed* (subbifacial), glabrous, stramineous.

DESCRIPTION: typical. *Thallus* pendulous, flaccid, subterete, compressed or angulate; cortex glabrous rugose and annularly ruptured, exposing cottonous medulla, stramineous; *primary branches* divaricate, dichotomous, sometimes echinate (max. length 35 cm.); *secondary branches* dichotomous, apices acuminate and darkening. *Apothecia* uncommon, lateral, small (max. diameter 2–6 cm.), marginate, thalline exciple rugose, disk chestnut, margins finally crenulate. *Spores* $5-10 \times 3.5-6 \mu$.

CONTINGENT PHASES: unobserved.

SUBSTRATA: On coniferous trees.

GEOGRAPHICAL DISTRIBUTION: Occurs rarely in the Boreal zone. It has been reported from the following localities in the Rocky Mountains: California (*Hall*), Colorado (*Brandege*), Bamff (*Macoun*), Mt. For-get-me-not, Elbow River (*Macoun*), British Columbia (*Macoun*). I have seen specimens from Divide Mt., 8000 ft., Montana (*Williams*), and Alpine, Colorado. The specimen in the U.S. Nat. Herbarium from Colorado, collected by Professor G. VASEY (referred to by TUCKERMAN), is unquestionably *Usnea cavernosa* Tuck. I have seen no fertile specimens from our area.

OBSERVATIONS: This plant is so rare in North American collections that its exact range is little known. It is undoubtedly a Boreal species, and may be looked for throughout the Rocky Mountains above 7000 ft. Its extreme flaccidity, and more or less compressed thallus, distinguishes it from *Usnea*,

which it in some degree suggests, on account of its annularly scarred thallus. The soft, cottonous, compressed medulla is at once seen, however, to be very unlike the terete, chondroid cord of *Usnea*. Like *thamnodes*, this species and *vulpina* have what has been considered a radial thallus. The structure cannot be said, however, to be strictly radial, and intergrades both individually and in species relation.

EVERNIA FURFURACEA (L.) Mann.

TYPE: Not indicated; the specimen on which LINNAEUS based his species is not in the Dillenian herbarium, Botanic Gardens, Oxford, England, "but two specimens which are there are smaller and sterile, though sufficiently typical" according to CROMBIE. According to WAINIO "*33 Lichen furfuraceus* = *Evernia furfuracea* Mann.," as represented in the Linnaean herbarium.

TYPICAL LOCALITY: "Europae."

ORIGINAL DESCRIPTION: "foliaceus decumbens furfuraceus: laciniis acutis: subtus lacunosus atris," Linn. Spec. Pl. 2:1146. 1753.

FIGURE: [DILL., Hist. Musc. pl. 21. f. 52. 1741]; HOFFM., Descript. et adnum. Lich. pl. 9. f. 2. 1790.

SYNONYMY: *Lichen furfuraceus* Linn. *ibid.*; *Evernia furfuracea* Mann. Lich. in Boh. obs. despos. suc. des. 105. 1825.

DIAGNOSIS: *Thallus* caespitose or subpendulous, compressed (bifacial) and *channeled*, *furfuraceous-isidioid*, *cinereous*.

DESCRIPTION: typical. *Thallus* prostrate, caespitose, or subpendulous, compressed, pliant, *channeled* below; cortex above furfuraceous to isidioid, below lacunose; above cinereous, below white, at length blackening; *primary branches* dichotomous, sub-pinnate (max. length 15 cm.); *secondary branches* much divided, apices furcate or tripartate. *Apothecia* marginal, subpedicellate, ample (max. diameter 1.7 cm.), disk chestnut. *Spores* $5.5-8 \times 3.5-5 \mu$.

CONTINGENT PHASES: reduced, sterile (boreal swamps in Transition regions).

SUBSTRATA: Coniferous and deciduous trees.

GEOGRAPHICAL DISTRIBUTION: Found throughout the Transition zone as far south as Bergen, New Jersey (*Eckfeldt*); Albany, New York; Pike Co., Penn.; Ohio (*Bogue*); Walker Mts., Smyth Co., Virginia; Grandfather (*Cummings*) and Crowden Mts., N.C.; Florida (*Calkins*); Tennessee (*Moore*); and Orizaba Mt., Mexico (*Stone*). Westward it extends to Minnesota (*Fink*). It reaches northward only to the lower limits of the Boreal zone, practically all alpine (over 3000 ft.) examples being referable to the following variety.

OBSERVATIONS: This species is found to intergrade with its variety where they meet on the mountain sides of the southern peaks; intermediate and atypical specimens having been examined from Grandfather Mt., S.C.; at Coahuila, and on Orizaba Mt., Mexico. Fertile examples of the species are rare, and the apothecia always smaller than in the variety.

EVERNIA FURFURACEA var. CERATEA (Ach.) Nyl.

TYPE: Not indicated; but the specimens on which the species was based are in the Acharian herbarium, Universitets Botaniska Institution, Helsingfors. These specimens have been kindly sent me for examination by Dr. FRED. ELFVING. The two labelled "var. *ceratea*" are typical fruited specimens, showing the characteristic "corniculato ramosis," and nearly smooth thallus. The specimens of the varieties β *nuda* and δ *scobisina* (see figure) were formerly indicated on the mounts by * and ‡, but these marks were either erased by ACHARIUS or some later worker, so that the exact identification of the (sterile) specimens referred to is in doubt. In any event, the specimens are referable to the species *furfuracea* rather than to the corniculate variety. The variety γ *scobisina* is indistinguishable from the species, being only a name for a more isidiod contingent phase, while *nuda* was not recognized in the *Methodus* (1803) as were the other varieties, but was first described in 1810. *Nuda* represents a contingent phase of *furfuracea* unworthy of recognition, transitional at best, though curiously enough the only one retained by Acharius in the *Synopsis* of 1814.

TYPE LOCALITY: Not indicated, but the above specimens are labelled "Svecia."

ORIGINAL DESCRIPTION: "thalli laciniis angustioribus suberectus corniculato-ramosis acuminatis supra incanis glabris nudijsculis."

FIGURE: none.

SYNONYMY: *Parmelia furfuracea* β *ceratea* Ach. Method. Lich. 2:255. 1803; *Evernia furfuracea* var. *ceratea* (Ach.) Nyl. Lich. Scand. 73. 1861.

DIAGNOSIS: Similar to last, *glabrous*, branches *subcylindrical* near apices, apothecia *ample*.

DESCRIPTION: typical; similar to last. *Thallus* more *gross*; cortex *glabrous* above, sometimes *verrucoso-papillate*, *rugose* or *pitted*, black *spermogones* frequent, branches distally *subcylindrical*, often linear. *Apothecia* common, at length crowded, *ample* (max. diameter 1.8 cm.). *Spores* as in last.

CONTINGENT PHASES: reduced branches with apices alike on both sides, entangled (*E. furfuracea* var. *Cladonia* Tuck.).

GEOGRAPHICAL DISTRIBUTION: Confined to alpine regions of the Boreal zone at altitudes of over 3000 ft. It occurs on the Appalachian range: in New Hampshire on the White Mts.; in Vermont I have seen it only from Mt.

Ascutney; in New York it is reported from Panther Mt., Catskills (*Harris*), and Mt. Whiteface, Adirondacks (*Peck*); and some of the material distributed from Grandfather Mt., N.C., by Miss CUMMINGS (Decades N. Amer. Lich. No. 2) is referable here. It undoubtedly occurs on Mt. Katadin, Me., and I have seen specimens from Ontario, Canada. The plants from the eastern United States are nearly always sterile or show rarely minute apothecia, entirely smooth and more "thyrsoid-entangled," and may possibly be worth recognition under the var. *Cladonia*¹² of TUCKERMAN, though they are in reality probably only reduced conditions of the more alpine fertile plant. In the Rocky Mountains I have seen specimens from alpine regions reaching 10,200 feet, extending from Colorado (Lake Moraine, Pikes Peak; Pagosa Peak, Veta Pass), New Mexico (Socorro Co., Mt. Gray), Arizona, Texas (*Parry*), southern California to Mexico (Coahuila, Monterey, San Luis Potosi,¹³ Mt. Orizaba).

OBSERVATIONS: This plant in its fruited condition, as already noted, strongly suggests morphologically the var. *vittata* Ach. of *Parmelia physodes*. It is also interesting to note that TUCKERMAN¹⁴ first considered the examples referable to his *Cladonia* nearest to ACHARIUS' *ceratea*.

Section: EUEVERNIA sect. nova.

Thallus bifacial, medulla stuppeous, compressed, non-chondroid

EVERNIA TRULLA (Ach.) Mont.

TYPE: Is in the Acharian herbarium, Universitets Botaniska Institution, Helsingfors, according to Professor FRED. ELFVING in litt. May 8, 1910.

TYPE LOCALITY: Peru, South America.

ORIGINAL DESCRIPTION: "thallo membranaceo subcaespitosa albido-pallescenti utrique nudo glabro subtus canaliculato, laciniis linearibus dichotomis; scutellis marginalibus cyathiformibus rufo-fuscis, margine subtusque crenulato-rugosis."

FIGURE: Method. Lich. pl. 4. f. 6. 1803.

SYNONYMY: *Parmelia trulla* Ach. Meth. Lich. 256. 1803; *Evernia trulla* Mont. C. Gay, Fl. Chil. 8:74. 1852.

DIAGNOSIS: *Thallus* caespitose decumbent, *compressed* (bifacial), glabrous, canaliculate, pale virescent.

DESCRIPTION: typical. *Thallus* caespitose, decumbent, compressed, canaliculate; cortex glabrous, glauco-virescent, darkening

¹² Synop. Lich. N. E., etc. 12. 1848. Type: No. 56, Fasc. 3, 4, Lich. Amer. Sept. exsiccati, 1854. Type locality: "Montium Alborum."

¹³ Material from here showed a few rhizinae.

¹⁴ Further enum. N. E. Lich. Bost. Jour. Nat. Hist. 3:300. 1840.

beneath; *branches* dichotomous. *Apothecia* lateral, subcyathiform, exciple rugose, disk chestnut-brown. *Spores* $11-16 \times 7-9 \mu$.

SUBSTRATA: On the ground.

GEOGRAPHICAL DISTRIBUTION: Mexico.

OBSERVATIONS: This rare North American plant has been only recorded from Mexico. It seems in every way logical that this species should therefore stand last of the *Evernias*, and next before the *Parmeliaceae* in our taxonomy. This relation has been assigned this genus by ZAHLBRUCKNER, with the removal of *Cetraria* into the *Parmeliaceae*, where it occupies a position preceding *Evernia*.

HUE records *Evernia intensa* Nyl.¹⁵ from Mexico. The species is apparently a chemical one, of which there is probably but little material. I have been unable to see the plant.

In closing this paper it is a great satisfaction to learn that at the Congress at Brussels *Linnaeus Species Plantarum* (1753) has been approved as the starting point for lichenological nomenclature. The labor involved here and in my *Usnea* paper in settling the priority of names is therefore not in vain.

For the opportunity to complete this paper I am indebted largely to Dr. N. L. BRITTON, who extended me during the past year a Garden Research scholarship, which was unfortunately cut short by ill health. To many others connected with the New York Botanic Gardens, to Dr. G. C. ALLEN, Dr. L. W. RIDDLE, Dr. FRED. ELFVING, Prof. BRUCE FINK, Dr. H. E. HASSE, DR. R. W. DRECHSLER, Mr. L. K. LUNT, and numerous other friends I am also most grateful.

THOREAU MUSEUM
CONCORD, MASS.

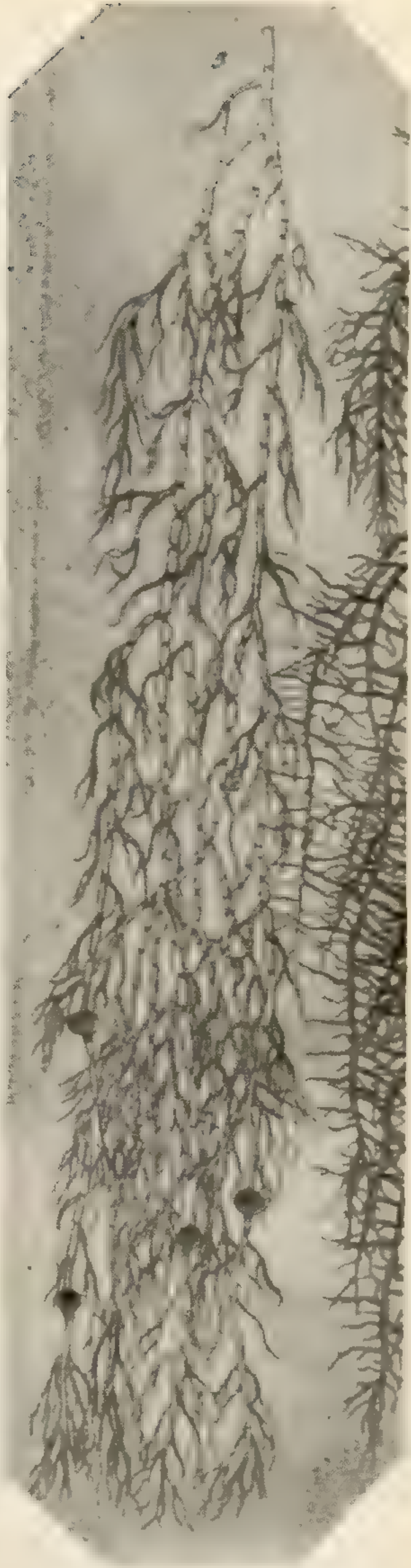
EXPLANATION OF PLATES XXIV AND XXV

- FIG. 1.—DILLENIIUS plate of *Evernia prunastri* (L.) Ach. (Lichenoides).
FIG. 2.—DILLENIIUS plate of *Evernia divaricata* (L.) Ach. (Lichenoides).
FIG. 3.—RETZIUS type of *Lichen arenarius* = *Evernia divaricata*.
FIG. 4.—DILLENIIUS plate of *Evernia furfuracea* (L.) Mann. (Lichenoides).
FIG. 5.—*Evernia Trulla* (Ach.) Mont. from a specimen in the U.S. Nat. Herb.
FIG. 6.—Acharian types of *Evernia furfuracea* and varieties (Borrera).
FIG. 7.—*Evernia furfuracea* var. *ceratea* (Ach.) Nyl. collected in Colorado by L. K. LUNT.

¹⁵ Flora 30:546. 1872; and Bull. Soc. Linn. Norm. 6:269. 1872.



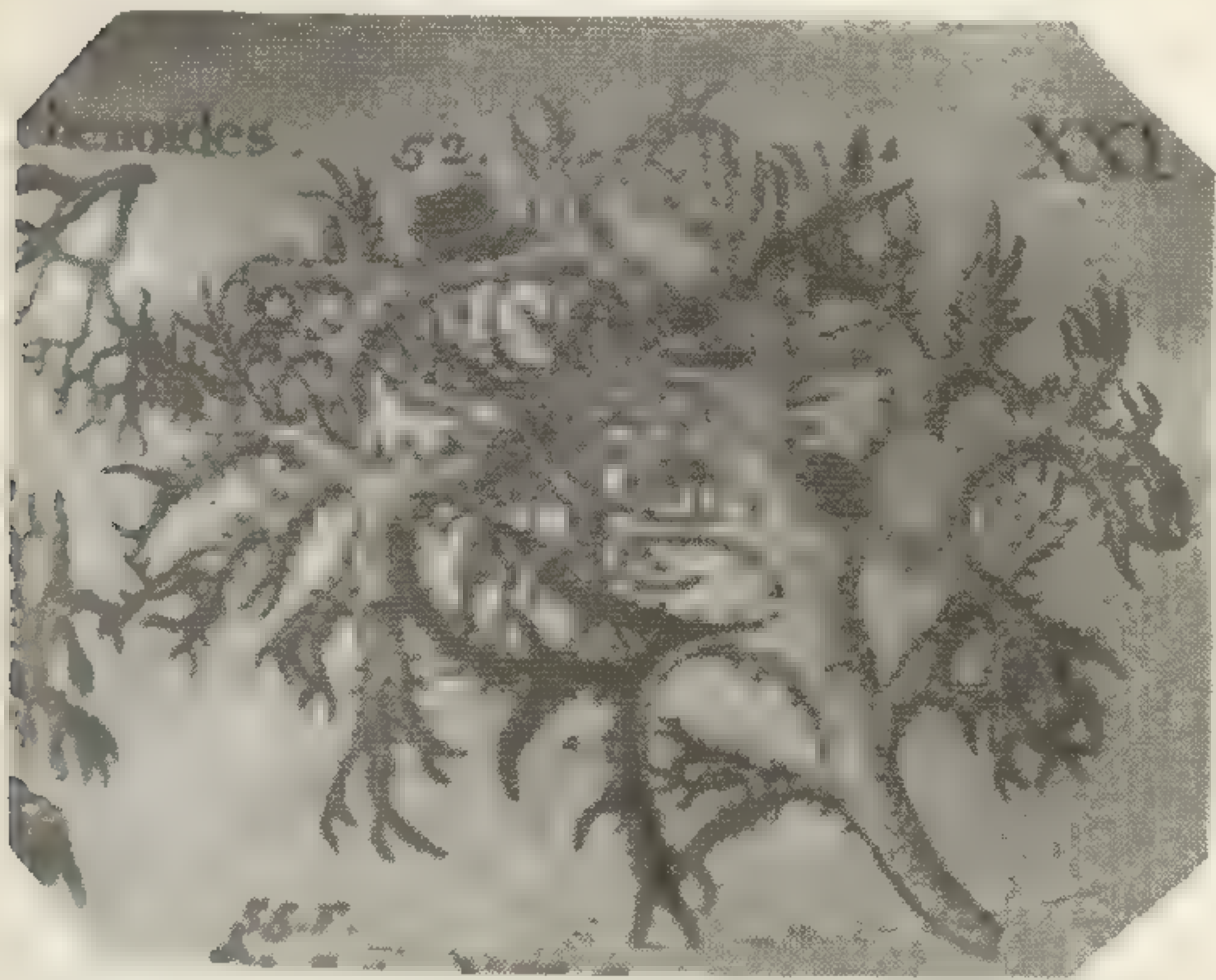
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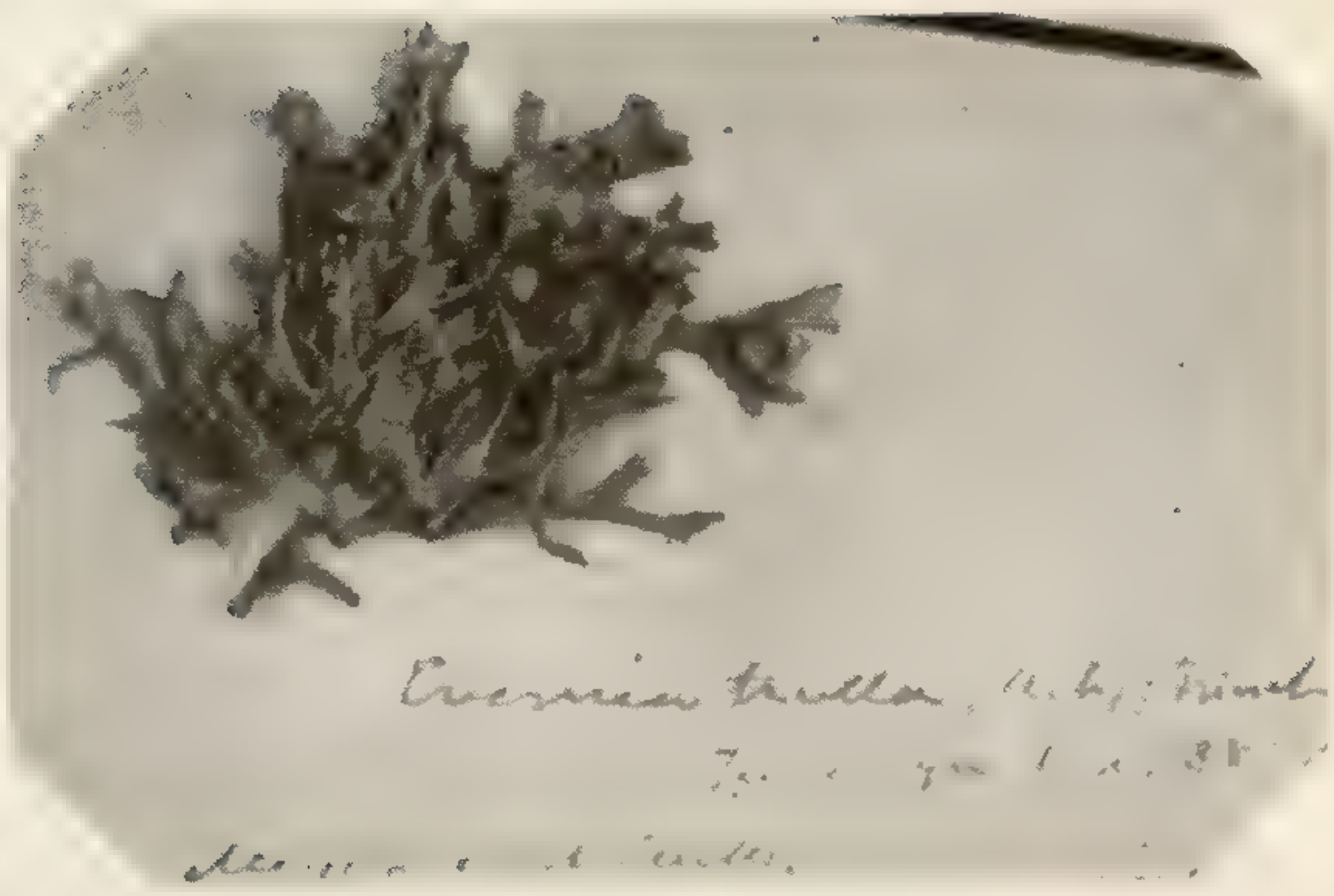
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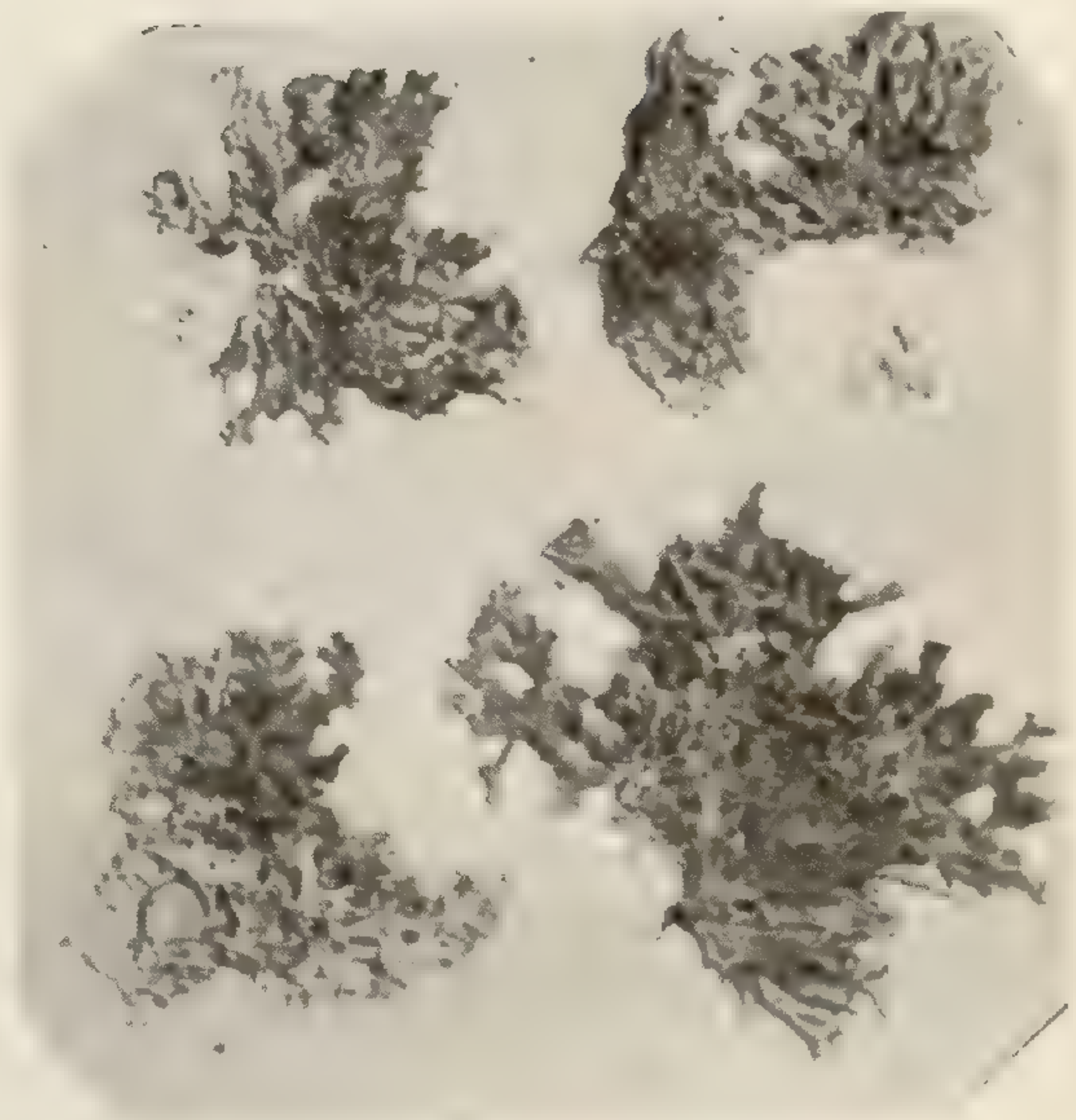
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7

HOWE on EVERNIA

IMBEDDED SEXUAL CELLS IN THE POLYPODIACEAE

MARGARET C. FERGUSON

(WITH PLATES XXVI AND XXVII)

About five years ago an assistant in the botanical laboratories of Wellesley College, Miss ANN REBECCA TORRENCE, was asked to prepare a set of slides, illustrating the development of the sexual organs in the ferns, for general class use. In looking over the slides which she had marked as valueless, I found several preparations showing an unusual origin of the egg cells. These slides were put aside with the expectation of publishing a note in the near future.

In February 1910, Miss JEAN WINSLOW, a student in my advanced course in cytology and comparative morphology, was puzzled by certain structures which she found in several of her preparations. The material was fixed and prepared for study by the student herself under the direction of the laboratory assistant, Miss EMILY P. LOCKE. Upon examining her slides, I found that they contained numerous instances of imbedded antheridia.

The fern prothallia used for class purposes are grown by the gardener. He sows, in clay saucers containing especially prepared soil, the spores of *Pteris* and *Adiantum*, some dishes containing only spores of *Pteris* and others containing spores of *Adiantum*. In both instances the structures about to be described were taken from cultures marked "Pteris," probably *Pteris cristata*; but since the spores of other species of *Pteris* are sometimes sown, I cannot state definitely the exact species of *Pteris* which was studied.

When the imbedded antheridia were discovered, I looked up the slides showing the deep-seated origin of eggs in *Pteris*, and we had a very interesting class demonstration and discussion.

At that time I said to the class that similar phenomena had never before been seen in a leptosporangiate fern; at least, if seen, the observations had never been published. Within a week I

had made the drawings which appear in connection with this note, but was detained from writing at that time. A little later, in looking over some back numbers of the current botanical literature, I ran across Miss BLACK's paper describing imbedded antheridia in *Dryopteris* and *Nephrodium*.¹ It is interesting that with no knowledge of Miss BLACK's work I had come to practically the same conclusion as that outlined in her paper regarding the origin and development of these unusual structures. I publish herewith exactly the same figures, without change or addition, as were prepared before Miss BLACK's paper was read. No prothallium containing unusual sexual organs was studied that did not also show normal archegonia and antheridia in all stages of development.

There can be no question as to the presence of an imbedded antheridium in these leptosporangiate ferns very similar to that found in the eusporangiates. Compare figs. 11 and 12 of this paper with Campbell's figs. 125 *D*, 128 *B*, 152 *D*.² The origin of these antheridia is not so obvious. There is no doubt that, as described by Miss BLACK, they may have practically the same origin as archegonia, but they may present transitional stages between normal antheridia and archegonia. Fig. 1 shows a normal young antheridium in which the first wall formed was not sufficiently concave to reach the basal wall, as is ordinarily but not invariably the case. Had the initial cell failed to protrude before the laying down of this cross-wall, such a structure would have been formed as that shown in fig. 2. Here the second wall formed, the dome-shaped cell, is much more prolonged than is usual. But the protrusion of the outer cell may be much less (fig. 3), or there may be no arching at all (fig. 4), when we would have what is recognized as an early stage in the development of a normal archegonium. Miss BLACK finds that arching occurs only in later stages of development, but in *Pteris* there is undoubtedly a greater or less arching of the initial cell in many cases, as if it were unde-

¹ BLACK, CAROLINE A., The development of the embedded antheridium in *Dryopteris stipularis* (Wild.) Maxon and "*Nephrodium molle*." Bull. Torr. Bot. Club 36: 557. 1909.

² CAMPBELL, D. H., Mosses and ferns. New York. 1905.

cided as to whether it should be an antheridium or an archegonium; but the arching in such cases is insufficient to make the resulting organ completely superficial.

The first wall laid down in the development of the imbedded antheridium is in the same plane as under normal conditions, but it may be deep-seated and little or not at all saucer-shaped (figs. 2, 3, 5). The second wall cuts out a central cell which may be very dome-shaped or may not be arched at all (figs. 2, 3, 5, 7, 8). The third wall follows in normal succession, cutting out the cover cell (figs. 5, 7, 8). The divisions occurring in the central cell of these antheridia in *Pteris* are somewhat different from those occurring in *Dryopteris* and *Nephrodium* as described by Miss BLACK. The first wall may sometimes be anticlinal and divide the cell into two equal cells, as is true under normal conditions (fig. 9a); but in the majority of cases observed the central cell of the entirely sunken antheridium was divided by two slightly oblique anticlinal walls into three cells lying in the same plane (figs. 7, 8).

Later stages in the development of the antheridium could not be traced beyond a question in the material at hand. But sooner or later a mass of cells occurs, from which the sperms are eventually produced. In order to meet the needs of the enlarged antheridium the one cover cell is replaced by a cell complex. As a rule, the mature imbedded antheridium is covered by a single layer of cells, but it may become two cells deep (fig. 10). In all cases observed, the imbedded antheridium is surrounded by a layer of cells much smaller than those which form the venter of an archegonium in the ferns, suggesting very strongly in their arrangement and appearance tapetal cells (figs. 10-12).

The size of the young, partially imbedded antheridia is practically the same as that of the normal antheridia, as is seen by a comparison of figs. 1 and 3, and figs. 5 and 6. But in later stages of development these unusual antheridia may become greatly enlarged. The more deeply sunken the antheridium the greater the size is apt to be at maturity. A normal, mature antheridium is shown in fig. 13. Compare this both as to position and size with the antheridia illustrated in figs. 11 and 12. Fig. 12 does not represent the largest antheridium observed. It was figured

rather to show that these organs not only may not protrude but that the cover cells may actually be depressed. Several antheridia much larger than this were observed. The sperm cells, while perfectly normal in appearance, are considerably larger than those developed under the usual conditions.

Imbedded antheridia were not found on the prothallia showing an unusual origin of the egg cells. In the case of the archegonia, the most frequent deviation from the normal gave two egg and two ventral canal cells lying in the plane of the longer axis of the archegonium (fig. 15). There is little doubt in this case that the more deeply imbedded egg and ventral canal cell were derived from the basal cell of the young archegonium. Ordinarily this cell contributes to the formation of the venter of the archegonium. In several instances the basal cell contained a beautiful, spherical mass of dense cytoplasm with a large nucleus, presenting the appearance of a large central cell before its division to form the ventral canal cell and the egg cell (fig. 14). The preparations studied showed egg cells that were unquestionably derived from other cells of the venter, but in these instances the sections were cut at such an angle as to render the figures unfavorable for reproduction.

There is no evidence that these deep-seated eggs or the imbedded antheridia were developed in response to dryness, as was the case in Miss BLACK's material. The two prothallia containing each seven or eight abnormal antheridia and the three prothallia showing several deep-seated eggs occurred in cultures from which a large amount of material was put up, and no other prothallia showed any deviation from the normal. Of course the fact remains that these particular prothallia may have been in positions of especial exposure, but, considering the method of culturing the prothallia, this is not probable.

I shall not enter into a prolonged discussion of the significance of these structures, since this has been so recently and so ably done by Miss BLACK. I wish simply to emphasize the point which she makes regarding the bearing of these phenomena on the question of the determination of sex in monoecious prothallia, and on the problem of vegetative fusion as described by recent writers.

In this connection the condition represented in fig. 9b is very interesting. Here we have apparently the first three cells of an archegonium, in which the central cell has developed directly into what is to all appearances a sperm cell. This leads us to inquire at what point in the development of a prothallium the sexual nature of its cells is determined. Are we not too much accustomed in our thinking to combine the idea of sexuality with form and position and definite organs? It may be that maleness and femaleness have no necessary relation to form or position or sexual organs, but that sperms and eggs are developed in relation to the sexual act or process, not as a necessary expression of sexuality. Should this be found to be true, then many cases of so-called vegetative fusion may come to be considered simply as instances of early or premature fertilization. To determine the point in the development of monoecious prothallia at which certain cells become endowed with sexuality, and the characteristic which makes them male or female, is one of the interesting but difficult problems which await solution.

WELLESLEY COLLEGE
WELLESLEY, MASSACHUSETTS

EXPLANATION OF PLATES XXVI AND XXVII

Unusual conditions in the development of the antheridia and the archegonia in *Pteris*.

FIG. 1.—A young antheridium in which the first wall laid down is very slightly concave.

FIG. 2.—A young, partially imbedded antheridium; the first wall laid down is parallel with the basal wall and not at all concave, while the second wall is very greatly arched.

FIG. 3.—A similar stage to that shown in fig. 2, but the antheridium is more completely imbedded and the outer cell arches but slightly.

FIG. 4.—The three-celled stage either of a normal archegonium or of an imbedded antheridium.

FIG. 5.—A later stage in the development of a partially imbedded antheridium; the cover cell has been cut out in the usual manner.

FIG. 6.—A slightly later stage in the development of a normal antheridium.

FIGS. 7, 8.—Practically the same stage of partially or wholly imbedded antheridia as that shown in fig. 6; their position is entirely that of young archegonia.

FIG. 9a.—A later stage in the development of a partially imbedded antheridium; the first division of the central cell was evidently the same as under normal conditions.

FIG. 9b.—An early stage in the development of a normal archegonium or of an imbedded antheridium; in this case the central cell has apparently given rise directly to a sperm cell.

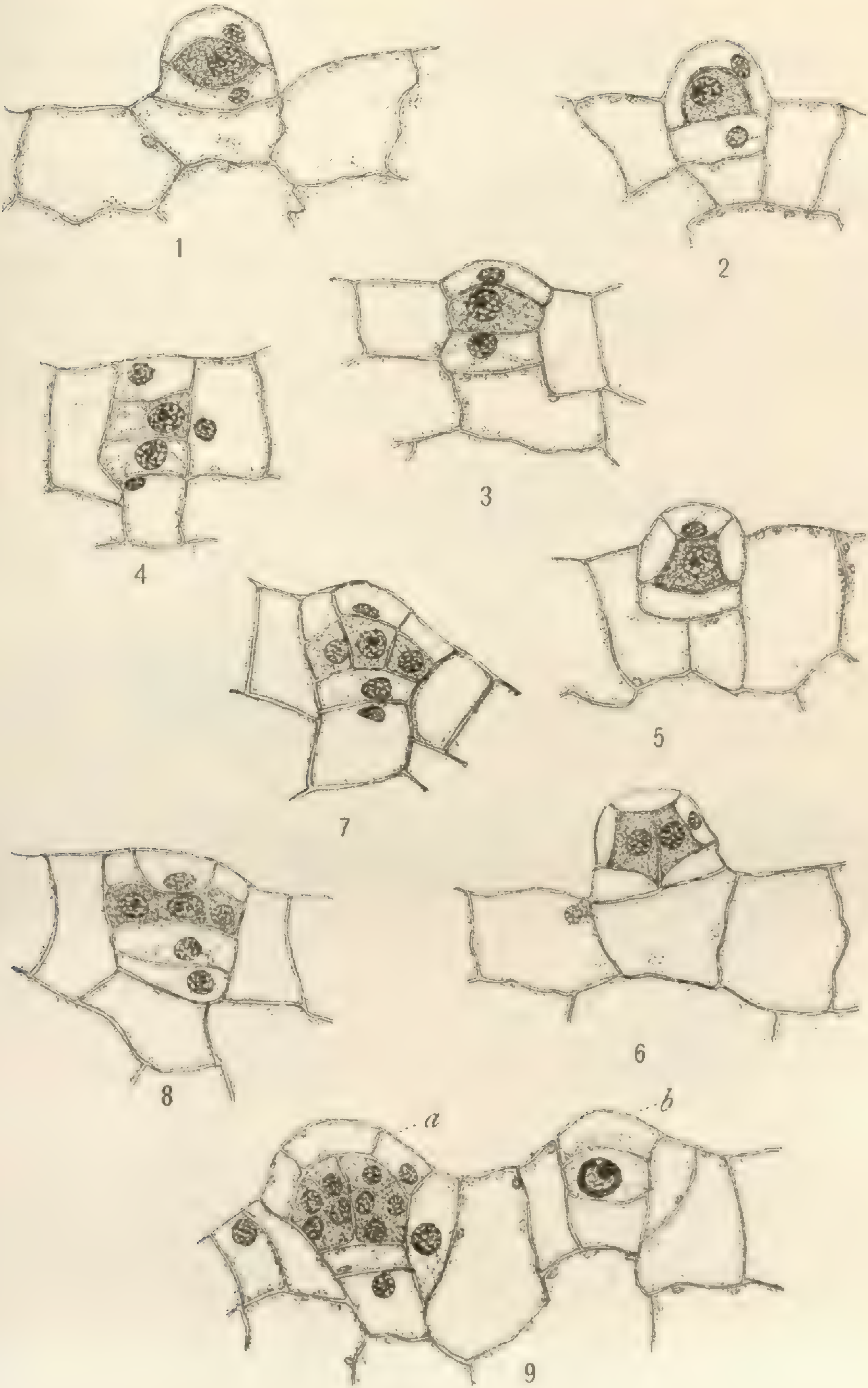
FIG. 10.—The sporogenous cells of an antheridium lying two layers of cells beneath the surface of the prothallium.

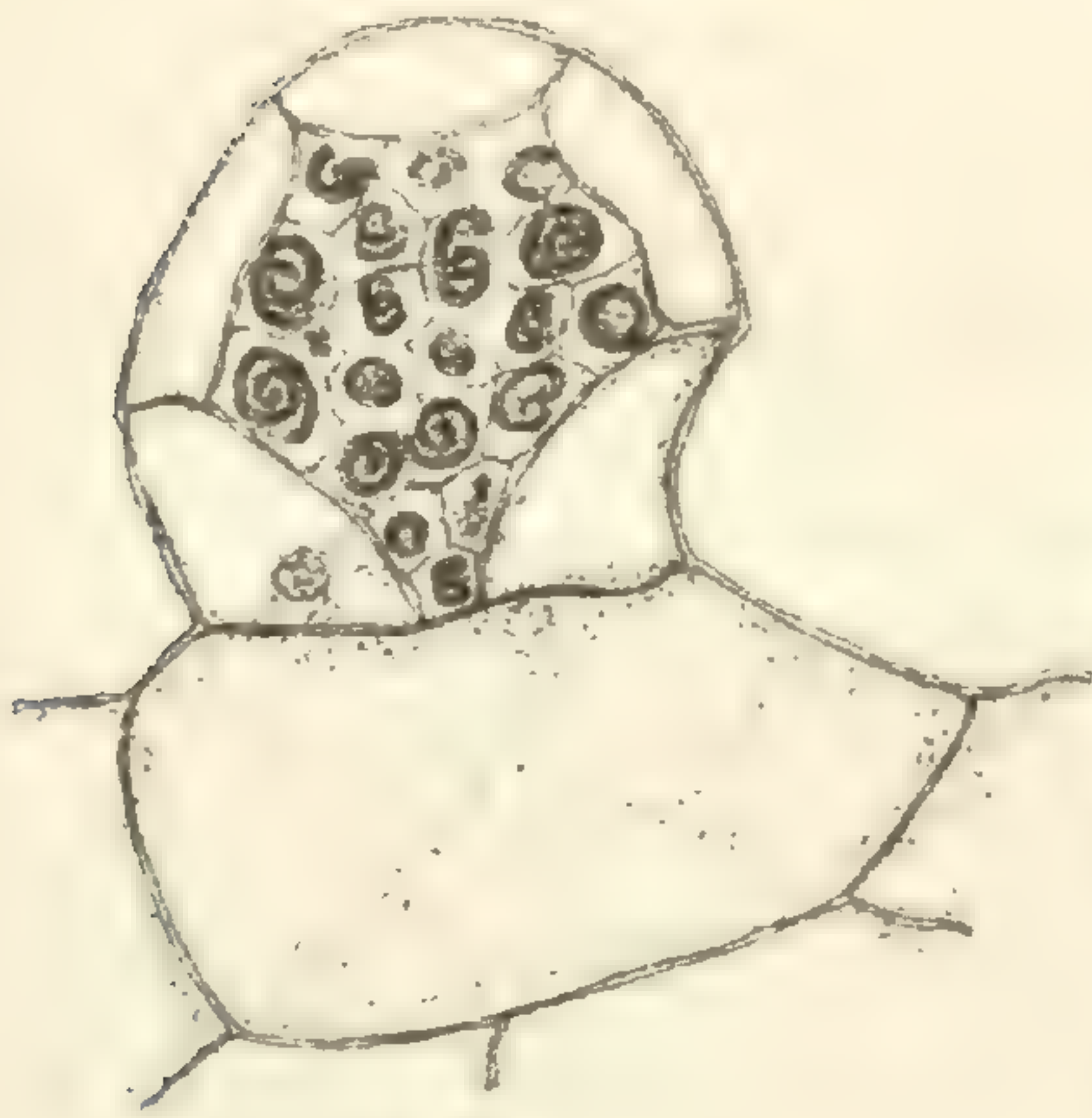
FIGS. 11, 12.—Two mature imbedded antheridia; both antheridia and sperms larger than those developed normally.

FIG. 13.—A mature, normal antheridium; note position and size as compared with those shown in figs. 11 and 12; these three antheridia were all taken from the same prothallium.

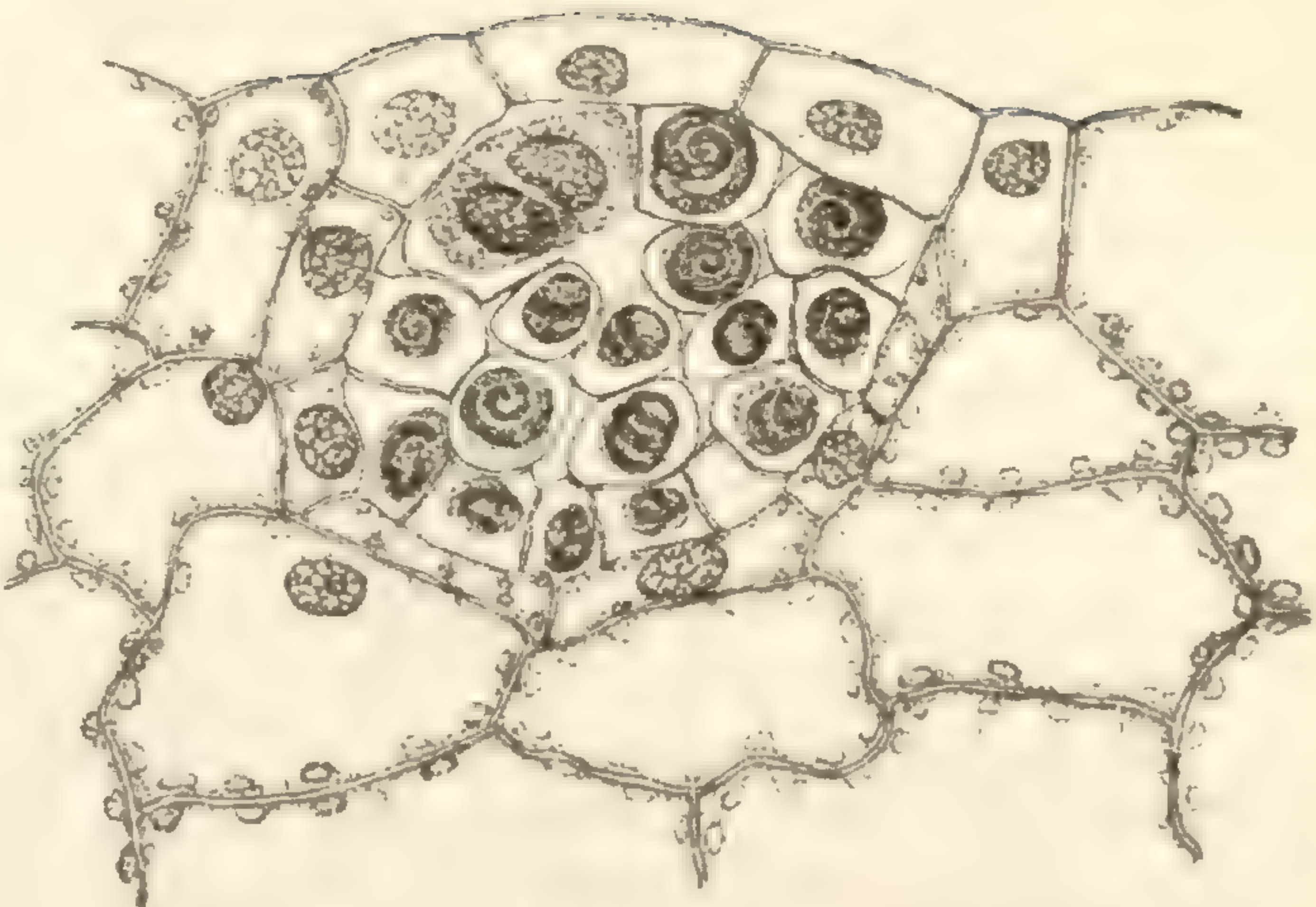
FIG. 14.—An archegonium normal in all respects except that the basal cell is greatly enlarged and contains either an egg or a protoplast which would later have divided to form a second egg and a second ventral canal cell.

FIG. 15.—An archegonium containing two egg and two ventral canal cells; the second egg and canal cells have evidently been derived from the basal cell.





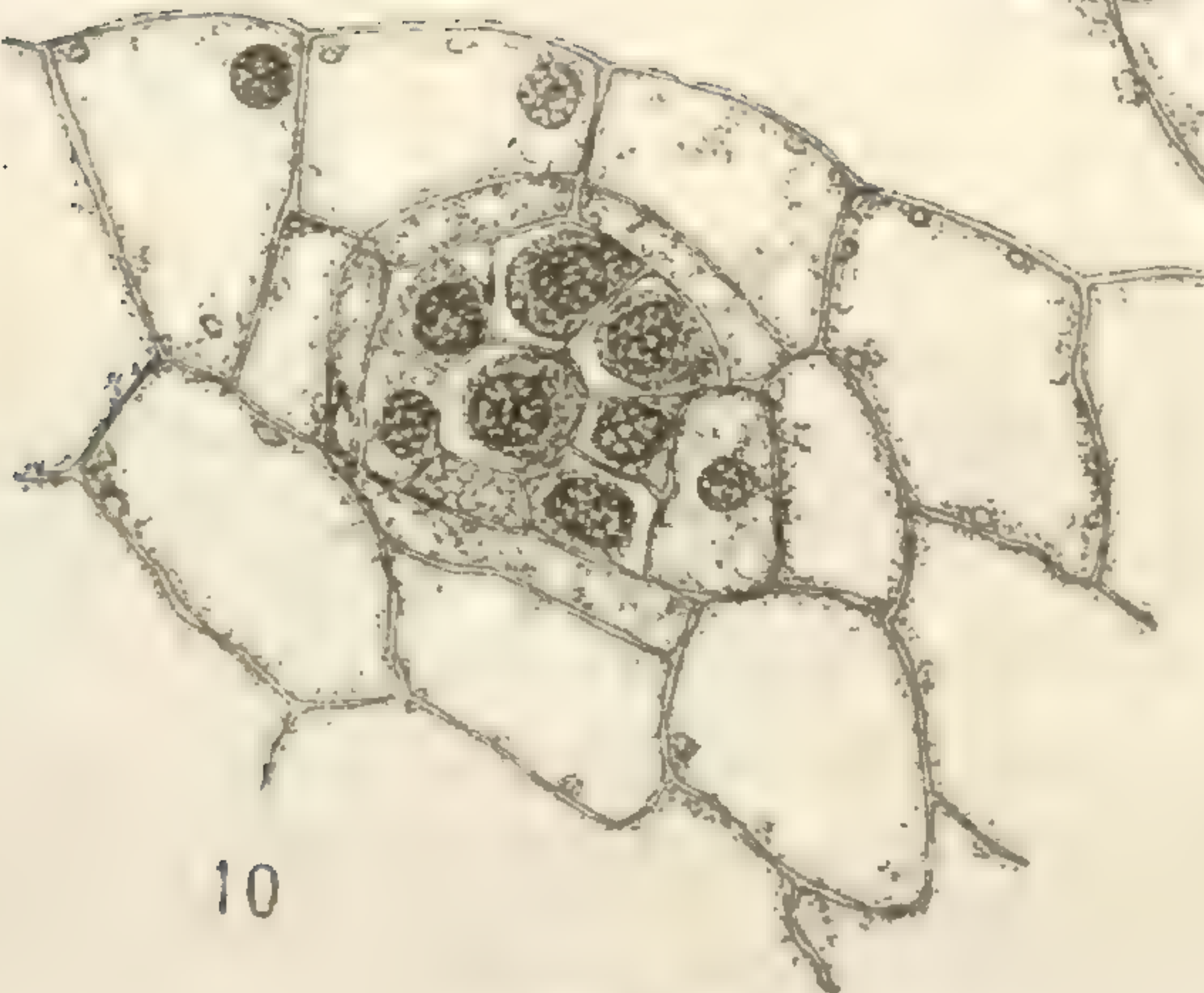
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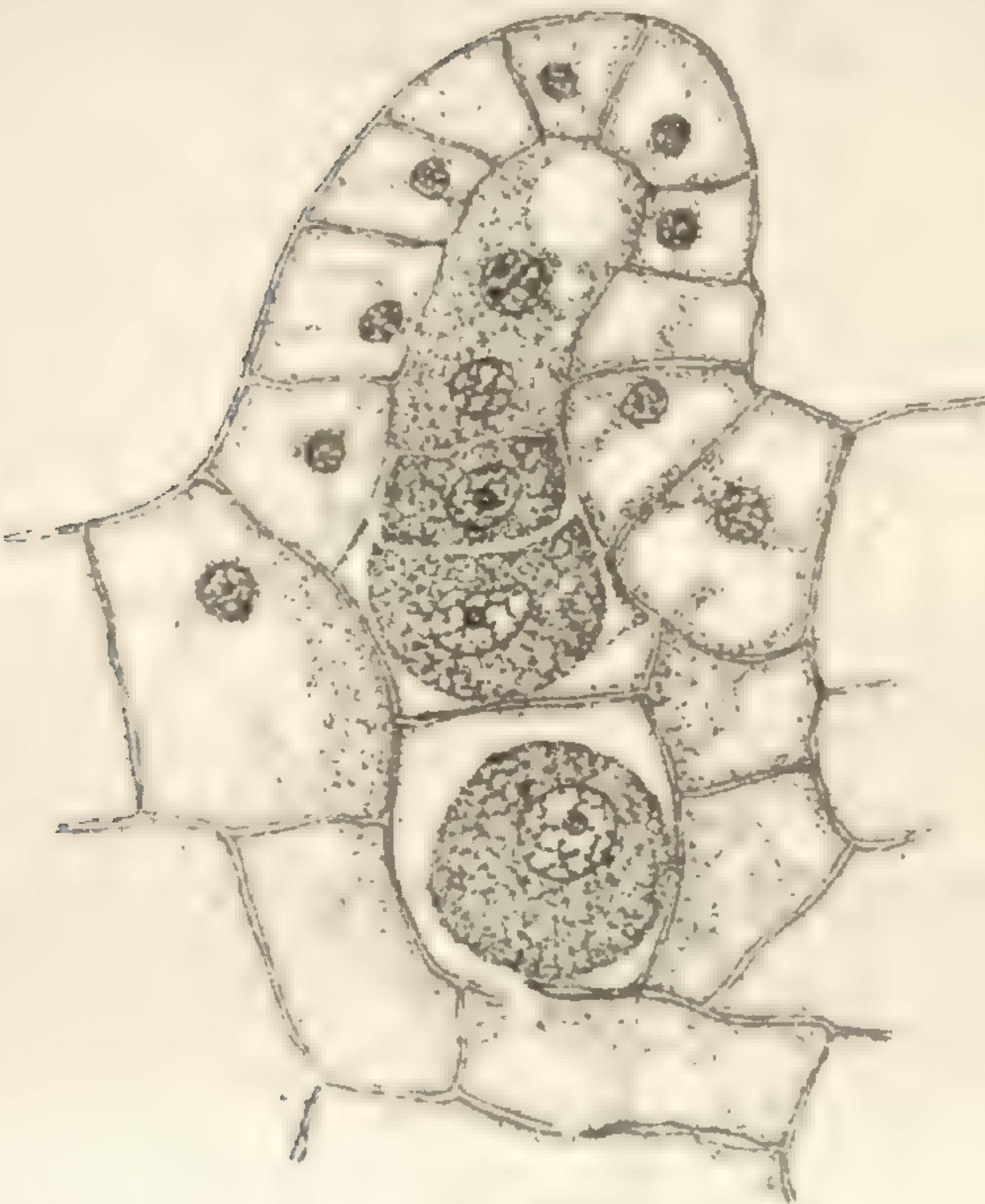
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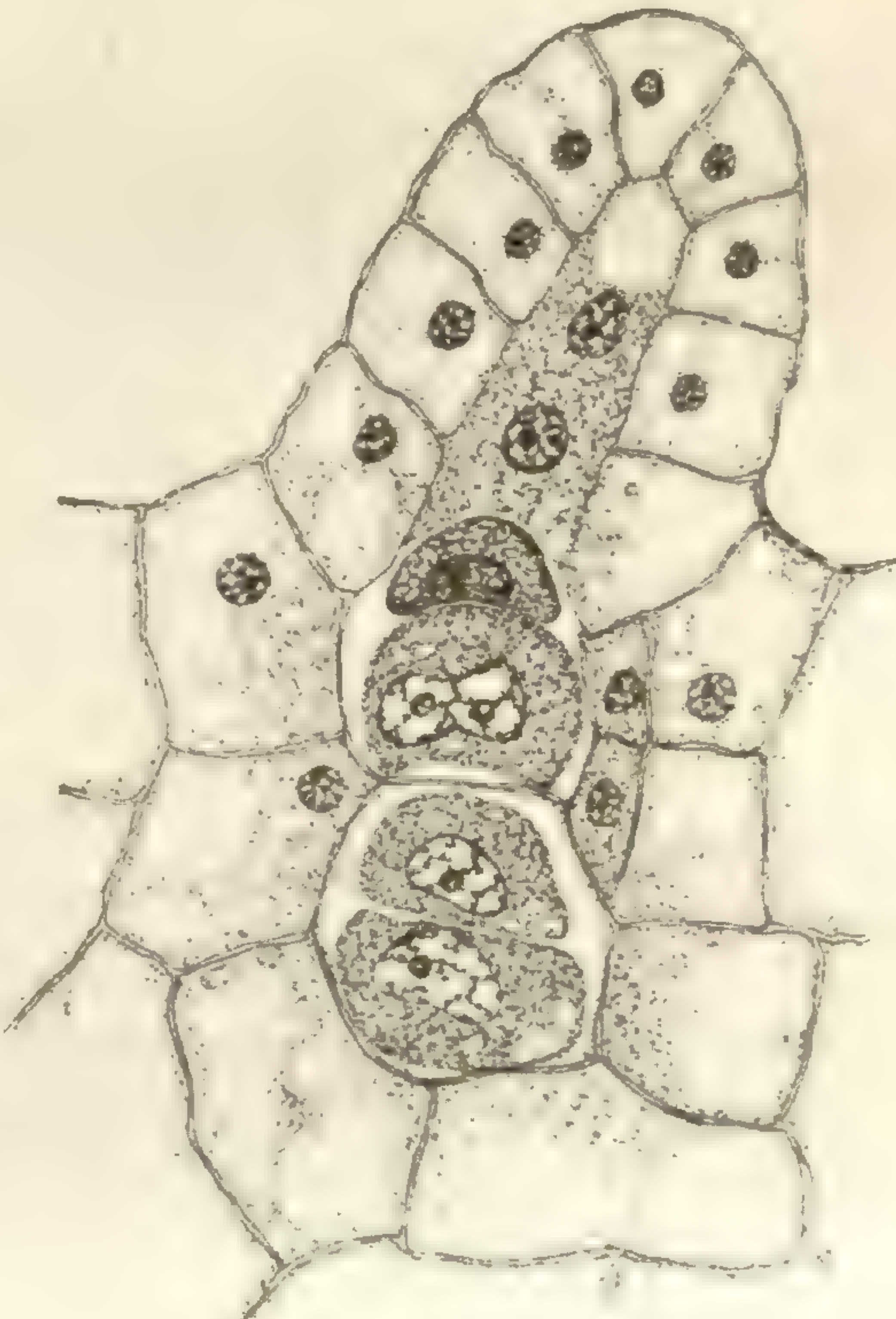
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15

AN AMERICAN LEPIDOSTROBUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 144

JOHN M. COULTER AND W. J. G. LAND

(WITH PLATES XXVIII AND XXIX AND THREE FIGURES)

The remarkable uncovering of the structure of paleozoic strobili and seeds during the last decade, chiefly from sections of English and French material, has brought to the American morphologist a feeling of disappointment that the extensive American Coal-measure deposits have yielded these structures only as impressions or casts. Extended inquiry has failed to discover such petrified material in any of the collections, so that its occurrence is evidently quite unusual.

A short time since there came into our hands, through the courtesy of Dr. STUART WELLER, of the Department of Geology of this university, a specimen of *Lepidostrobus*, the strobilus of *Lepidodendron*, that was evidently petrified. It had been collected in 1900, in a coal pocket in Warren County, Iowa; and in January 1911 came into the possession of Professor JOHN L. TILTON, of Simpson College, Indianola, Iowa, who brought it to this university, and in whose collection a portion of the sectioned cone is to be found.

The specimen is not a complete strobilus, but a fragment from near the upper end, broken at an angle above, and squarely across below. As a consequence, if the strobilus was heterosporous, all evidence of the megasporangia had disappeared with the missing lower portion. The fragment is 6 cm. long and 5 cm. in diameter at base, and all the structures proved to be very well preserved except the axis (figs. 1 and 2), which had been almost completely destroyed and replaced by calcite and pyrites. The strobilus was a mature one, which had fallen and remained in the water or moist soil, for rootlets had penetrated between the sporophylls here and there, and the rootlets in turn had been attacked by a fungus. Nearly all of the sporangia are empty, only a few spores being occasionally in place, but masses of spores occur in many places between the sporophylls.

The general structure of *Lepidostrobus* is well known, but it seemed worth while to section this American specimen and to record the results. We have not attempted to refer it to any described species, as this would involve us in unfamiliar details. The only purpose is to describe briefly the structure of the first American Coal-measure strobilus to be sectioned, so far as we can discover.

The stalks of the crowded sporophylls stand approximately at right angles to the axis of the strobilus (fig. 2), and are triangular in cross-section, the keeled abaxial face fitting between two sporangia on the sporophylls below (fig. 4). This stalklike base of the sporophyll is about 20 mm. long, and broadens widely as it joins the lamina (fig. 5), whose plane is approximately at right angles to that of the stalk. The lamina is 20 mm. long, extending below the plane of the stalk in a broad triangular base and narrowing rapidly above into a long acuminate extension (fig. 8). The result is that each lamina overlaps several others above, the surface appearance of the strobilus resembling that of a roof covered with pointed tiles; and the broad, wavy, and notched base interlocks with the sporophylls below. The sporangia are thus very closely and heavily incased, and all the structures of the strobilus are fitted solidly together. A single and very simple vascular strand traverses the stalk of the sporophyll and continues into the lamina, consisting of a small central group of protoxylem elements (fig. 20), completely invested by a narrow zone of vessels of larger caliber, and this in turn by a broad zone of delicate tissue which abuts against the cortex.

In the narrow space between the distal end of the sporangium and the base of the lamina, the ligule appears as a small conical body arising from a shallow pit (fig. 16). This relationship of the ligule to the sporangium and the lamina of the sporophyll seems to be constant among the ligulate forms, the distance from the base of the sporophyll in this case being determined by the great radial extension of the sporangium. The cells of the sporophyll immediately below the pit of the ligule are much longer than the other cells, and radiate from the ligular pit. These radiating and elongated cells perhaps indicate that in the early stages of the sporophyll considerable photosynthetic work was done by the ligule.

The cells of the ligule itself are small and almost isodiametric; and its tip is invariably withered.

The most characteristic feature of *Lepidostrobis* is the radially elongated sporangium, which extends along the whole adaxial face of the stalk of the sporophyll. In our specimen the sporangium is 17 mm. long and 2.5–3 mm. broad, attached along the central axis of the stalk by a narrow connection, and bulging pouchlike beyond the sides of the stalk, until the latter broadens into winglike extensions near the lamina. Only in the distal region of the sporangium is there any evidence of a "subarchesporial pad," which appears in section as a broad and low dome of tissue (fig. 12); there is no evidence of any radiating sterile tracts within the sporangium.

The most notable feature of the sporangium, aside from its radial extension, is its dehiscence (fig. 6). A series of transverse sections indicates this very clearly (figs. 9–13), and also served as the basis of a restoration. The sporangium dehisces longitudinally along the median line for a little more than half its length from the base, and then the line of dehiscence forks and is represented in the distal half of the sporangium by two diverging lines, which leaves between them a large triangular flap of the sporangium wall. In most cases the structure of the outermost layer of sporangium wall is well preserved, consisting of the characteristic "prismatic palisade-like cells" (figs. 17 and 18). The wall, under pressure of the adjacent structures, is quite definitely angled (figs. 9 and 16), and at these angles the palisade-like cells are conspicuously elongated, and within the angles there are usually traces of the more delicate inner wall layers. No special mechanism of dehiscence was discovered, although it is reasonable to suppose that one exists in the case of this singular dichotomous or tri-radial dehiscence. Since the distal ends of the sporangia abut against the heavy interlocking bases of the laminae, it is altogether probable that the continuation of the median longitudinal dehiscence becomes mechanically impossible.

It is to be regretted that the basal part of the strobilus was not secured, so that the question of heterospory might have been answered. The spores observed are probably microspores, and their appearance is sufficiently indicated in fig. 19.

The fungus referred to above as accompanying rootlets that had penetrated among the sporophylls presents stages that seem worthy of record. The mycelium is abundant and wide branching, and suggests that of a phycomycete, since no cross walls are apparent except in a few cases, and these cases might be only such



FIG. 22



FIG. 21

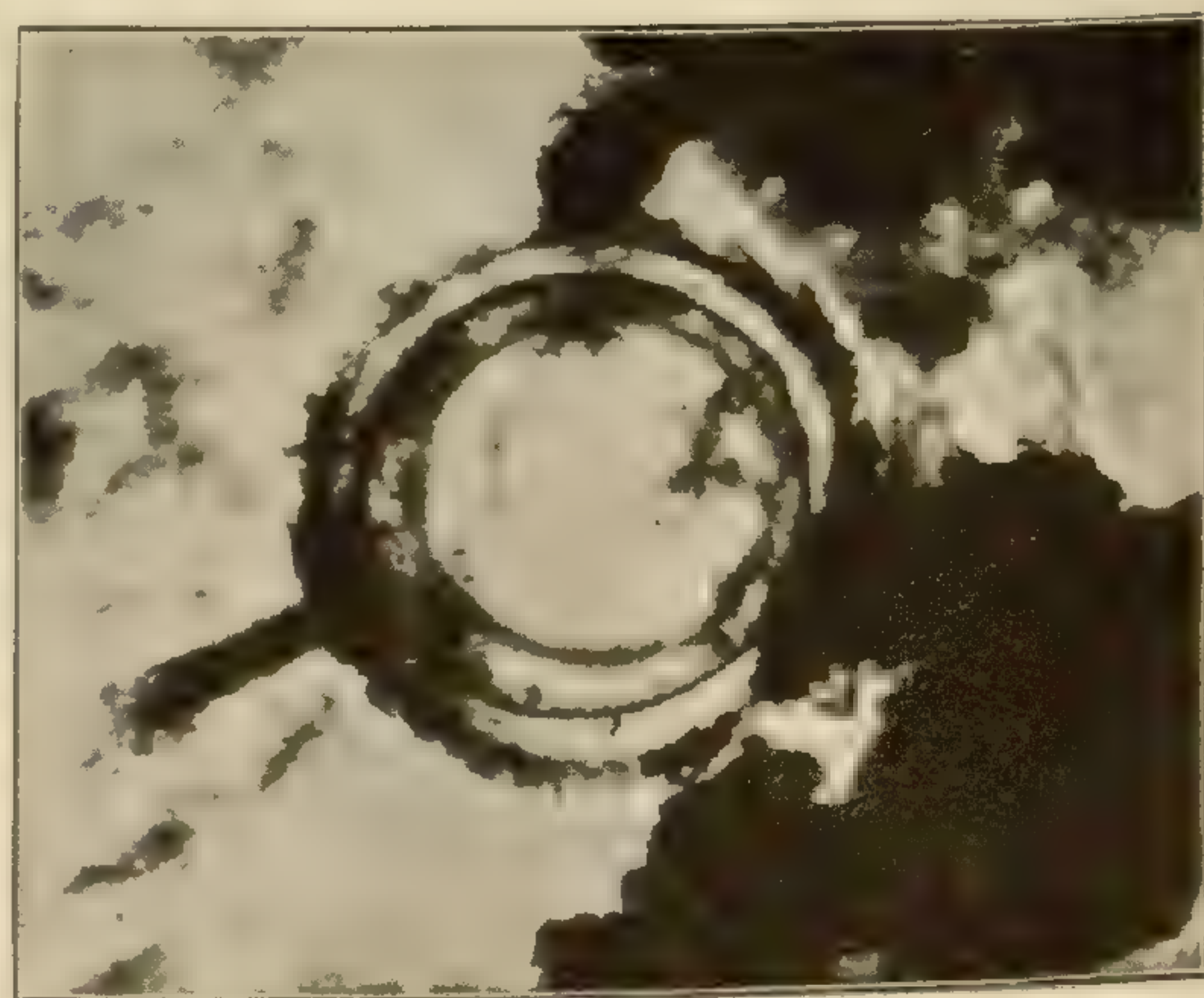


FIG. 23

FIGS. 21-23.—Fig. 21, Swollen end of hypha, suggesting a young oogonium; $\times 475$; fig. 22, Hyphae showing two oogonia; $\times 475$; fig. 23, Photomicrograph of fertilized egg (?) of fungus; $\times 141$.

as appear among phycomycetes. In many instances the hyphae bear what are evidently zygotes; and such stages as that shown in fig. 21 suggest the development of a sex organ. The situation represented in figs. 22 and 23 furthermore suggests that the fungus had oogonia and antheridia. However, it is fully realized, as suggested by Dr. HASSELBRING, to whom our preparations were submitted, that such data may be insufficient to determine the fungus with definiteness; it may be an oomycete; or it may not even be



5



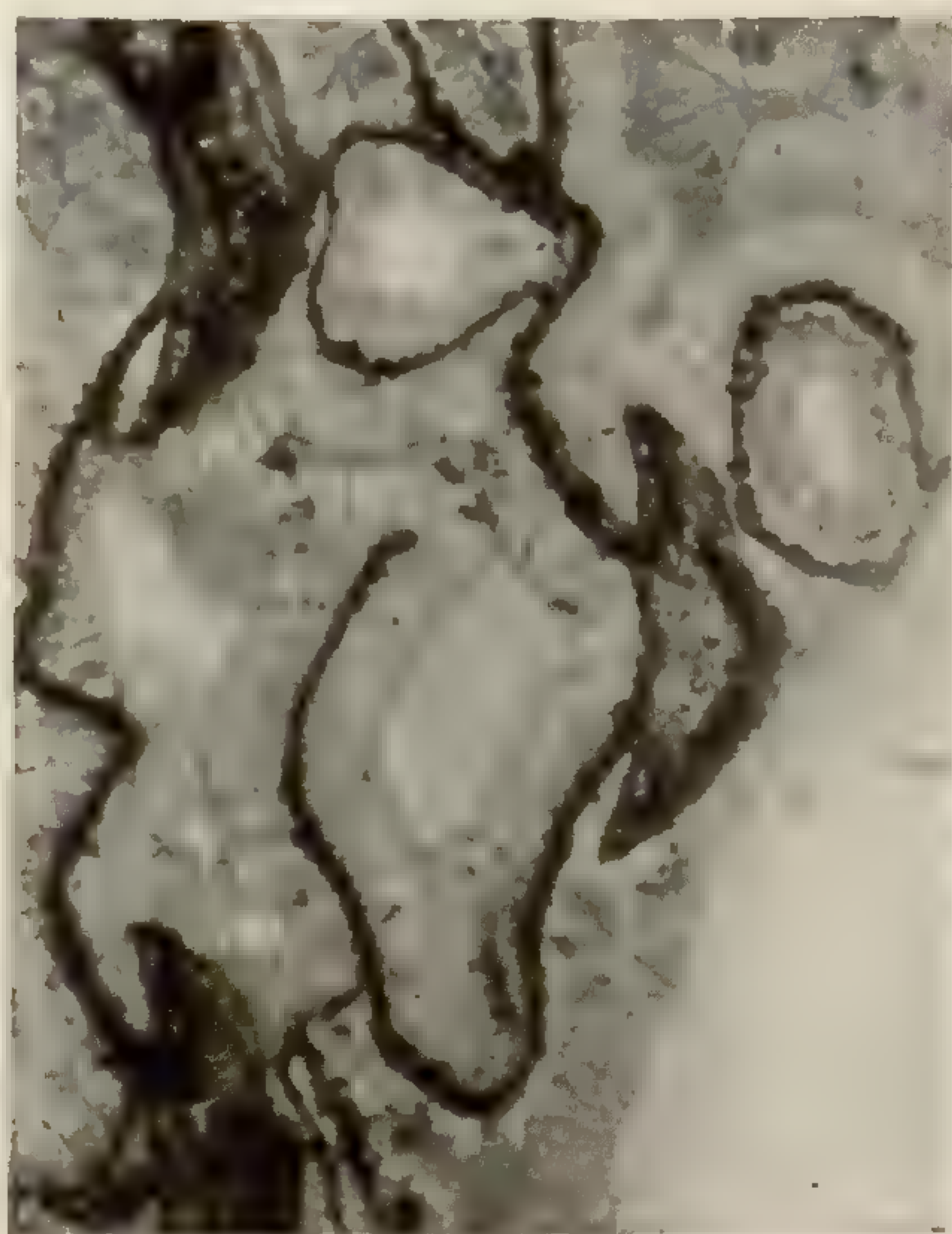
6



7



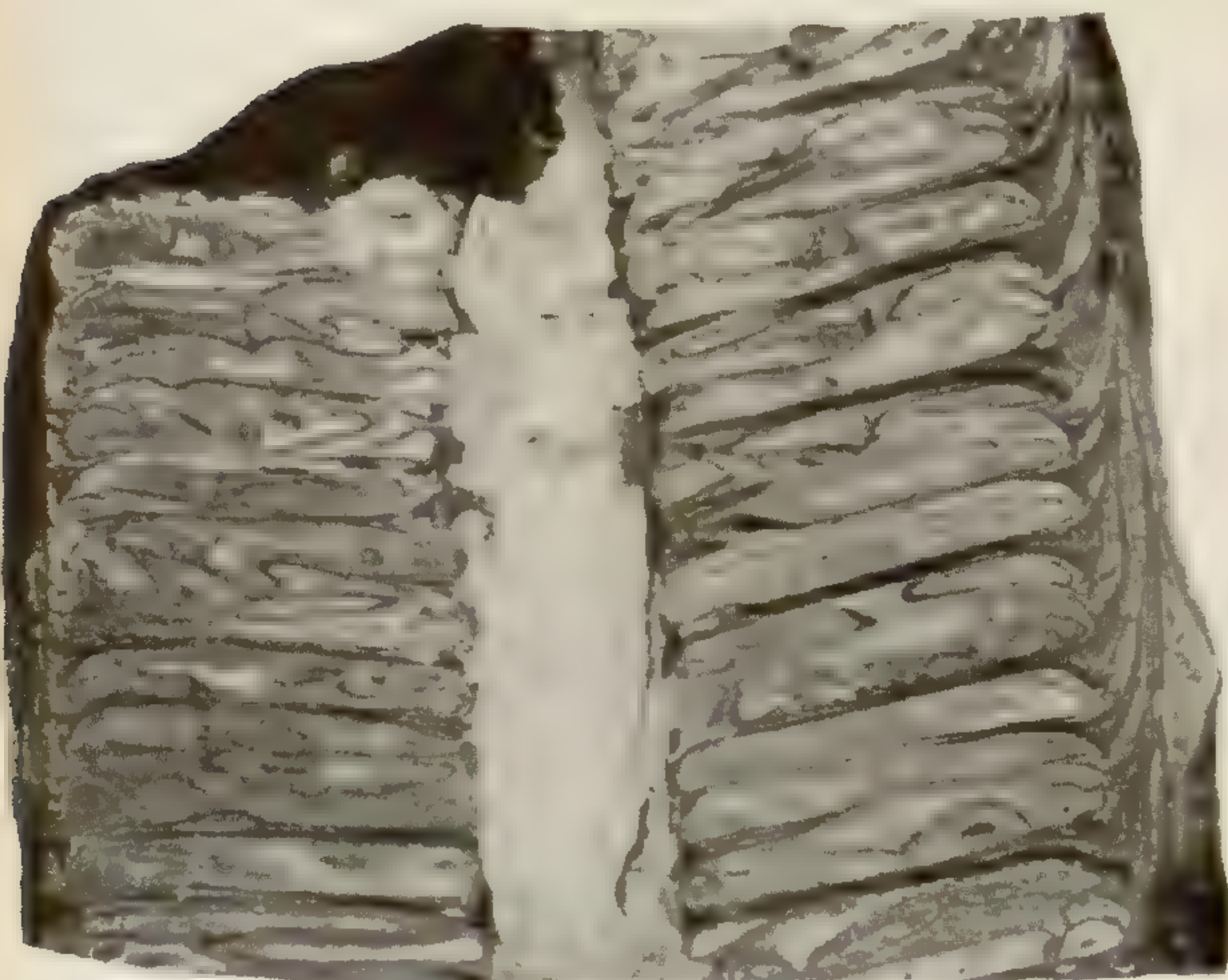
8



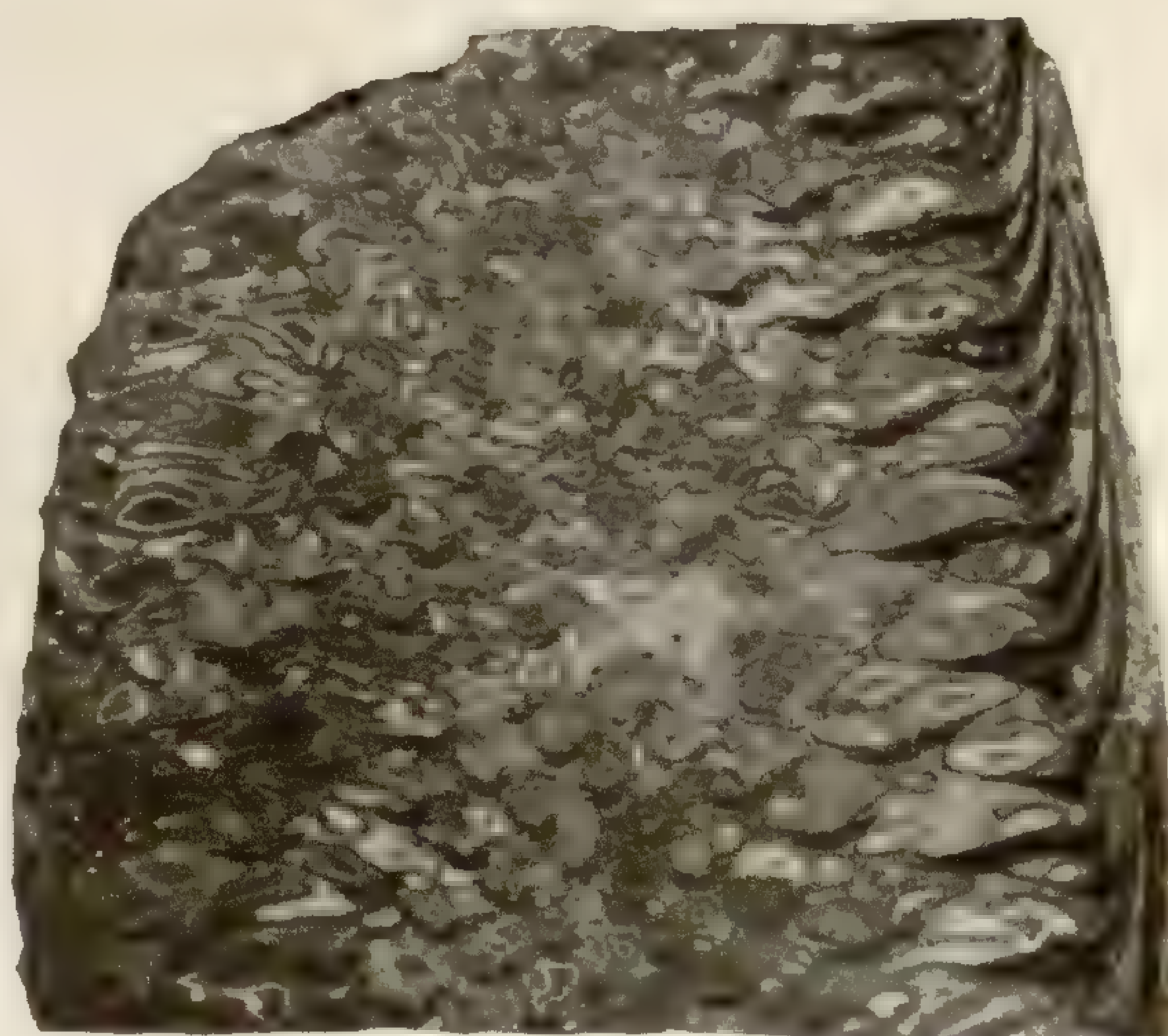
4



1

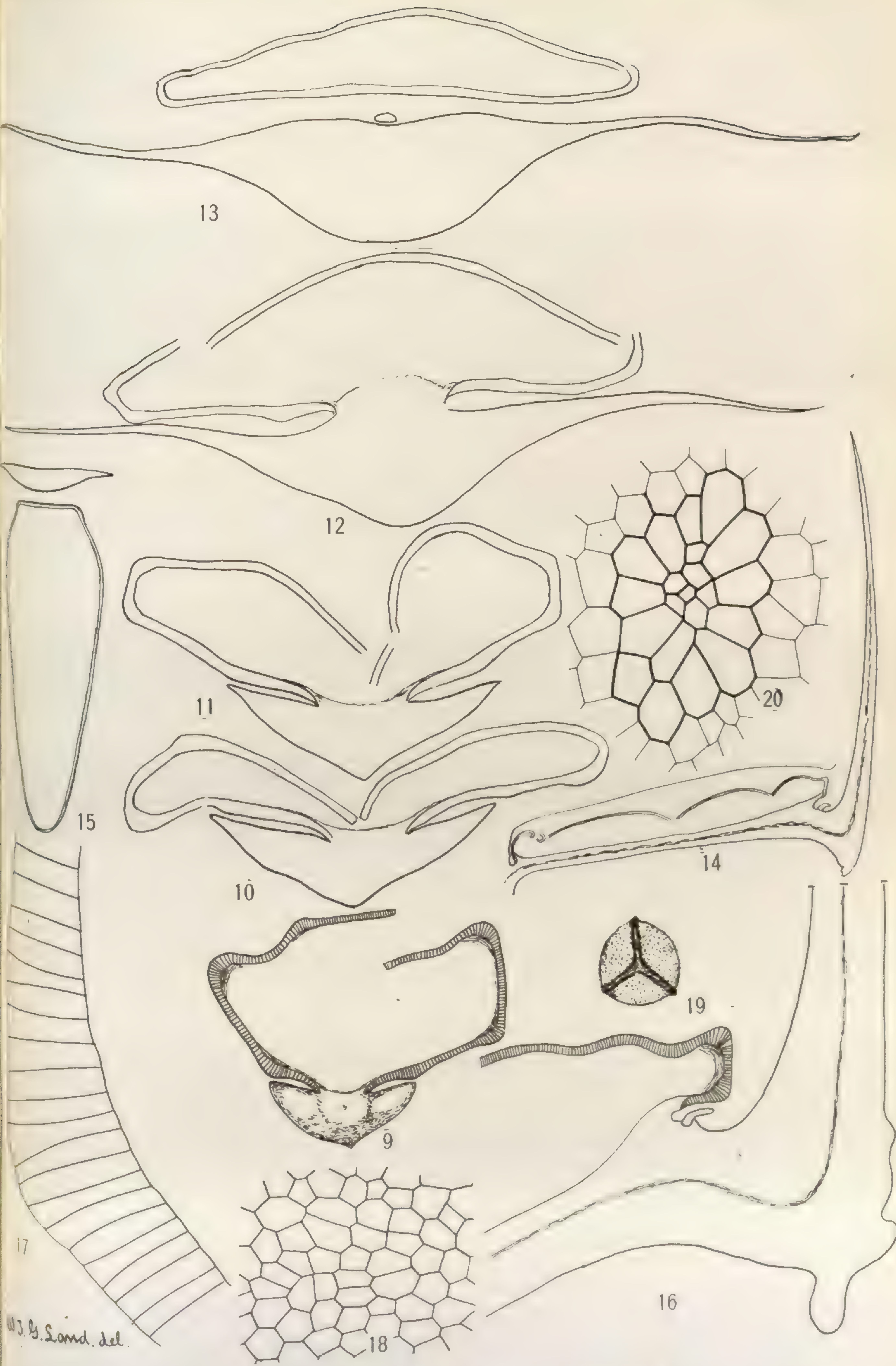


2



3

COULTER & LAND on LEPIDOSTROBUS



W.S. Land. del.

COULTER & LAND on LEPIDOSTROBUS

a phycomycete; but whatever it is, it became associated with rootlets that penetrated among the sporophylls of fallen strobili of *Lepidodendron*.

THE UNIVERSITY OF CHICAGO

EXPLANATION OF PLATES XXVIII AND XXIX

PLATE XXVIII

- FIG. 1.—Transverse section of strobilus; $\times 1$.
 FIG. 2.—Median longitudinal section of strobilus; $\times 1$.
 FIG. 3.—Tangential section of strobilus; $\times 1$.
 FIG. 4.—Transverse section of sporophyll 10 mm. from axis; $\times 12.5$.
 FIG. 5.—Abaxial view of sporophyll, from a reconstruction in plaster; $\times 2.5$.
 FIG. 6.—Abaxial view, showing dehiscence of sporangium; $\times 2.5$.
 FIG. 7.—Lateral view of sporophyll, showing relation of sporangium and ligule; $\times 2.5$.
 FIG. 8.—Abaxial view of lamina of sporophyll; $\times 2.5$.

PLATE XXIX

- FIG. 9.—Transverse section of sporophyll 1 mm. from axis; $\times 12.5$.
 FIG. 10.—Transverse section of sporophyll 6 mm. from axis; $\times 12.5$.
 FIG. 11.—Transverse section of sporophyll, showing triradiate dehiscence; $\times 12.5$.
 FIG. 12.—Transverse section of sporophyll near distal end; $\times 12.5$.
 FIG. 13.—Transverse section through sporophyll, ligule, and free distal end of sporangium; $\times 12.5$.
 FIG. 14.—Median longitudinal section through a sporophyll from basal region of strobilus, showing ligule and path of vascular strand; $\times 2.25$.
 FIG. 15.—Median longitudinal section of sporangium parallel with the axis of the sporophyll; $\times 2.25$.
 FIG. 16.—Median longitudinal section through ligule, showing general relations of parts; $\times 58$.
 FIG. 17.—Section through sporangium wall, showing the palisade-like cells; $\times 229$.
 FIG. 18.—Section of sporangium wall parallel with its surface; $\times 229$.
 FIG. 19.—Microspore (?); $\times 475$.
 FIG. 20.—Detail of xylem of vascular bundle of stalk of sporophyll, showing central protoxylem; $\times 475$.

SUGGESTIONS CONCERNING THE TERMINOLOGY OF SOIL BACTERIA

JACOB G. LIPMAN

The period 1890–1910 has been one of notable progress in soil bacteriology. It is marked, on the one hand, by the appearance of KRAMER'S book¹ and, on the other, by the publication of LÖHNIS' handbook.² A comparison of these two works will show not only a rapid increase in the body of facts relating to soil bacteria, but also a series of more or less successful attempts to arrange these facts in an orderly fashion. There have been created in this manner a number of terms that are to designate certain groups of physiological functions or reactions, like nitrogen-fixation, nitrification, denitrification, sulphate-reduction, etc.

As we inquire into the meaning of the different terms thus created, we find much that is indefinite and confused. We find, likewise, that other terms, while definite enough as to their meaning, are too unwieldy for use in the lecture room. For instance, the term "denitrification," already well established in our terminology, is not at all definite. The earlier investigators employed it to designate the reduction of nitrates,³ irrespective of the fact whether the reduction products were nitrites, ammonia, nitrous oxide, or nitrogen gas. Latterly there has been a tendency to restrict the use of the term to the complete reduction of nitrates, involving the liberation of nitrogen gas, or at most of nitrous and nitric oxides. KAYSER⁴ and after him LÖHNIS⁵ have attempted to distinguish between complete and partial reduction of nitrates by employing the terms "direct denitrification" and "indirect denitri-

¹ Die Bakteriologie in ihren Beziehungen zur Landwirtschaft. Vol. 1. Wien. 1890.

² Handbuch der landwirtschaftlichen Bakteriologie. Berlin. 1910.

³ GAYON and DUPETIT, Recherches sur la réduction des nitrates par les infiniment petits. Station Agronomique de Bordeaux. Nancy. 1886.

⁴ Microbiologie Agricole, p. 117.

⁵ Handbuch der landwirtschaftlichen Bakteriologie, p. 447.

fication." It is needless to say that these terms are not only too long, but when taken together with "Nitratreduktion" and "Salpeterassimilation," as employed by LÖHNIS,⁶ they are far from removing the existing confusion.

In the same way the terminology relating to the formation of nitrogen compounds by microorganisms out of elementary nitrogen is not at all satisfactory. The terms "Stickstofffixierung," "Stickstoffsammlung," and "Stickstoffassimilation" are used interchangeably in the German publications. The English terminology, with its "nitrogen-fixing," "nitrogen-gathering," and "nitrogen-assimilating" bacteria, is as unwieldy as the German "Stickstofffixierende Bakterien," or the French "microbes fixateurs d'azote." To make matters worse, there has crept into American publications⁷ the use of "nitrification" and "nitrifying" as synonymous with "nitrogen-fixation" and "nitrogen-fixing," respectively.

Almost as much confusion exists in the designation of other physiological reactions. One is uncertain in these days whether "methane bacteria" are organisms capable of decomposing cellulose with the formation of methane, or are merely organisms capable of oxidizing methane to water and carbon dioxide. It is difficult to decide, at times, whether the term "sulphur bacteria" refers to the organisms capable of oxidizing hydrogen sulphide partly, or to those capable of oxidizing it completely. Other examples of indefiniteness or confusion may be found in the terminology of sulphate reduction, hydrogen formation and oxidation, and ammonia production and transformation.

The foregoing examples will suffice to show that there is need for more rigid definition and classification in the domain of soil bacteriology. Indeed, this need is so pronounced that the writer has been led to prepare the present paper in spite of his desire not to introduce striking innovations, and in spite of the knowledge that any proposed change in the terminology already existing will be criticized. The writer would add here, however, that it is not his intention to propose any change either morphological or physiological in the general classification of bacteria. It is his wish,

⁶ *Op. cit.*, pp. 477-478.

⁷ See FLETCHER, "Soils."

merely, to systematize the designations of certain types of physiological reactions, and to arrange them so as to provide for future development. In doing this he has found it necessary to create a few new terms and to modify the meaning of old terms. The proposed arrangement of some of the more important groups of soil bacteria is as follows:

GROUPS OF SOIL BACTERIA ARRANGED IN ACCORDANCE WITH THEIR
PHYSIOLOGICAL FUNCTIONS

Ammono-bacteria

amino-
pepto-
proteo-

De-ammono-bacteria

-amino
-pepto
-proteo
-nitri
-nitra

Nitro-bacteria

nitri-
nitra { ammono-
 nitri-

De-nitro-bacteria

-nitri
-ammono
-nitrioxo
-nitraoxy

Proteo-bacteria

ammono-
amino-
pepto-
proteo-
nitri-
nitra-

De-proteo-bacteria

-pepto
-amino
-ammono

Azoto-bacteria

azo-
rhizo-

De-azoto-bacteria

amino-azo
ammono-azo
nitra-azo
nitri-azo

Sulpho-bacteria

sulphid-
thio-

De-sulpho-bacteria

-sulphite
-sulphid

Ferri-bacteria

ferro-

DEFINITIONS

Ammono-bacteria.—Organisms capable of producing ammonia out of nitrogen compounds.

Nitro-bacteria.—Organisms capable of oxidizing nitrogen compounds to nitrites, nitrates, or both.

Proteo-bacteria.—Organisms capable of transforming nitrogen compounds into protein.

Azoto-bacteria.—Organisms capable of changing elementary into combined nitrogen.

De-ammono-bacteria.—Organisms capable of transforming ammonia into nitrogen compounds other than nitrites or nitrates.

De-nitro-bacteria.—Organisms capable of reducing nitrates to nitrites, ammonia, nitrous or nitric oxide.

De-proteo-bacteria.—Organisms capable of transforming protein into more simple cleavage products.

De-azoto-bacteria.—Organisms capable of liberating elementary nitrogen from nitrogen compounds.

Sulpho-bacteria.—Organisms capable of oxidizing hydrogen sulphide to elementary sulphur, sulphites, or sulphates.

De-sulpho-bacteria.—Organisms capable of reducing sulphates to sulphites or sulphides.

Ferri-bacteria.—Organisms capable of transforming ferrous into ferric compounds.

CORRESPONDING TERMS

Ammonification

Nitrification

Proteofication

Azotofication

Sulphofication

Ferrification

Deammonification

Denitrification

Deproteofication

Deazotofication

Desulphofication

Deferrification

Of the eleven groups of bacteria named above, eight consist of organisms concerned in the transformation or increase of combined nitrogen. The ammono-bacteria consist of amino-ammono, pepto-ammono, and proteo-ammono, according to the source of the ammonia. It will be noted that the first part of the combined term refers to the initial product and the second part to the final product. Thus, proteo-ammono-bacteria are organisms capable of forming ammonia out of protein. It is evident, of course, that a single organism may be able to produce ammonia out of both peptone and protein, and it could be designated, therefore, as pepto-ammono and likewise as proteo-ammono. Similarly, the nitro-bacteria include the nitri- and the nitra-bacteria. The latter in their turn may consist of ammono-nitra and nitri-nitro, the assumption being in this case that there are species capable of oxidizing ammonia directly to nitrates.

The proteo-bacteria would naturally include a large number of species, among them the nitrate, ammonia, and amino assimilating species. While objections will probably be raised against the creation of this very general group, it must be recognized that the terms ammono-proteo or nitra-proteo are more consistent than "nitratassimilierende" or "ammonassimilierende." Moreover, these terms should supplement the term "proteofication," a very compact and logical designation of the transformation of various nitrogen compounds into protein.

The azoto-bacteria should include all of the nitrogen-fixing species. According to the proposed terminology, they would consist of the azo-bacteria, that is, the non-symbiotic nitrogen-fixing bacteria (freilebende stickstofffixierende Bakterien) and the rhizobacteria, that is, *Ps. radiculicola*. The azo-bacteria would in their turn consist of *Clostridium Pastoriannum*, *Azotobacter*, and miscellaneous species already known or still to be discovered. The proposed classification is elastic enough to allow the presence in the azo group of azo-ammono- or azo-nitro-bacteria, should it ever be definitely shown that elementary nitrogen may be directly transformed by certain species into ammonia or nitrate. No serious objection should be raised against the proposed use of azoto, azo, and rhizo. They are not only an improvement on the unwieldy terms at present in use, but are quite in keeping with the term azotofication, whose acceptability will hardly be disputed.

Turning now to the terms de-ammono, de-nitro, de-proteo, and de-azoto, we find them to be the opposites of the corresponding ammono, nitro, proteo, and azoto. Just as ammono designates the *appearance* of ammonia, so de-ammono designates the *disappearance* of ammonia. Now ammonia may disappear by being converted into amino-compounds, peptone, or protein; hence, de-ammono-amino, de-ammono-pepto, de-ammono-proteo. Also in this, as in every other case, the first part of the compound term designates the initial and the second part the final product. The terms de-ammono-nitri and de-ammono-nitra were not included in this group, because they properly belong to the nitro group (ammono-nitri and ammono-nitra).

The meaning of de-nitro has been modified to correspond to

nitro. It will be remembered that nitrifying bacteria, according to the accepted definition, are organisms capable of changing ammonia into nitrites and nitrates. If it be true, as it is claimed by KASERER, that there are organisms capable of oxidizing elementary nitrogen directly to nitrates, they should be included under the azoto-bacteria, the true nitrogen-fixing bacteria. Hence, nitrification deals properly with the transformation of nitrogen compounds, more strictly speaking, the *oxidation* of combined nitrogen. Now, since *denitrification* is a *reduction of combined nitrogen*, it should not include processes where *elementary* nitrogen is formed. The latter are the opposite of azotofication (nitrogen-fixation), and should therefore be included under deazotofication. In other words, KAYSER'S and LÖHNIS' direct *denitrification* would become deazotofication under the proposed terminology, and their indirect denitrification would properly become denitrification. The advantages of the proposed arrangement are so evident that further discussion is hardly necessary.

The next group of de-proteo-bacteria would naturally include the organisms of decay and putrefaction, and the term employed here should therefore refer to dissimilation processes. It is evident at the same time that many de-proteo-bacteria would also be proteo-bacteria and *vice versa*. Objection may be raised for this reason to de-proteo, as well as to proteo; nevertheless, because of their supplementing the very convenient terms proteofication and deproteofication, they should be retained.

The group of de-azoto-bacteria would include all species capable of breaking down nitrogen compounds with the evolution of elementary nitrogen. Starting with amino-compounds, ammonia, nitrates, or nitrites, we could have amino-azo-, ammono-azo-, nitra-azo-, and nitri-azo-bacteria. As was already indicated above, the direct denitrifiers would be designated here as nitri-azo- or nitra-azo-bacteria. Similarly, the organisms capable of oxidizing ammonia with the evolution of elementary nitrogen would be designated as ammono-azo-bacteria.

We come finally to the sulpho-bacteria and de-sulpho-bacteria, organisms concerned with the oxidation of hydrogen sulphide and elementary sulphur on the one hand, and of reducing sulphates

and sulphites on the other. The method of classification has been sufficiently outlined above to make it unnecessary to go into further detail here. It should be pointed out, however, that the proposed terminology could be extended to embrace many other physiological functions and reactions. It would be made to include the appearance and disappearance of methane, of hydrogen, of carbon monoxid, of sugars, amino-compounds, alcohols, organic acids, etc. Terms like dextro-propio or dextro-butyro should not be difficult to understand, nor many other compound terms that will readily suggest themselves to the reader.

The writer is aware of imperfections existing in the proposed grouping of some of the species; he feels, however, that in spite of these imperfections his suggestions deserve careful consideration at the hands of his colleagues. Should the present paper do no more than create a critical discussion of the existing terminology his work will not have been in vain.

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NEW BRUNSWICK, N.J.

BRIEFER ARTICLES

NOTE CONCERNING THE DISCOVERY OF THE NUCLEUS

Historical reviews generally refer the discovery of the nucleus to ROBERT BROWN, perhaps adding that before BROWN's work the nucleus had occasionally been figured, but that the authors attached so little importance to the structure that usually it is not even mentioned in the text. BROWN himself cites several of these instances.

A quite forgotten paper by F. J. F. MEYEN, published in *Linnaea* (1827),¹ however, gives an account of the nucleus of *Spirogyra*, which for accuracy of observation and clearness of detailed description leaves little to be desired. A somewhat briefer account, similar in essentials, appeared a year later in a little monograph entitled *Untersuchungen über den Inhalt der Pflanzenzellen*.² Neither publication being commonly accessible, a paragraph from the latter is reprinted here.

Es wird hier am rechten Orte sein nochmals auf den Inhalt der Zellen, in der Gattung *Spirogyra*, aufmerksam zu machen. Wir beobachteten nämlich, dass mitten in den Zellen dieser Pflanze ein plattgedrücktes rundes Zellchen, durch äusserst feine verästelte Fäden an der innern Fläche der Zelle befestigt, aufgehängt ist. Es hängt dieses Organ mit den platten Flächen parallel den Grundflächen der Zelle oder des Utriculus der *Spirogyra*, und zeigt bei der mikroskopischen Ansicht von Oben eine längliche schmale Figur, etwa $\frac{1}{4}$ bis $\frac{1}{3}$ der Länge des Querdurchmessers der Zelle haltend. Das Organ selbst ist fast durchsichtig und ungefärbt; eine grosse Menge von äusserst feine und sich verästelnden Fasern verlaufen von verschiedenen Punkten desselben meistens büschelförmig nach der innern Fläche des Utriculus, woselbst sie sich abermals ansetzen, um jenes Organ, gleichsam wie eine Spinne in ihrem Gewebe, in der Mitte des Utriculus fest zu halten. Es schien mir, als wären es stets 4-6 dergleichen Büschelchen feiner Fasern, die sämmtlich, nach verschiedenen Seiten verlaufend, das Zellchen in der Mitte des Schlauchs befestigen. Die Fasern selbst sind wohl die feinsten, die bis jetzt im ganzen Pflanzenreich beobachtet worden sind, sie sind ungefärbt, durchsichtig und daher sehr leicht zu übersehn. Ihrer grossen Feinheit wegen vermag man bei einer 300 maligen Vergrösserung an ihnen nichts mehr zu beobachten, als

¹ Ueber das Genus *Spirogyra* Lk., und über die Bewegung und Metamorphose der *Sp. princeps* insbesondere. *Linnaea* 2:428. 1827.

² Berlin, 1828, p. 55.

ihre Verästelung nach der Schlauchmembran zu. Die über dieses Organ gemachten Beobachtungen sind folgende: Durch Einwirkung von Weingeist und kochendem Wasser wird das längliche Organ ganz kugelförmig. Auch wird es kugelförmig, wenn die Pflanze ihren individuellen Lebenslauf vollendet hat und sich auflösen anschickt, alsdann reissen die Fasern allmählich sämmtlich entzwei, und das Organ selbst fällt aus der Mitte zur Seite, und nach Eröffnung der Zelle, durch Fäulniss, tritt es selbst zur Zelle hinaus. Zu dieser Zeit erscheint in jeder kugelförmigen Zelle, wozu sich jenes längliche Organ umgewandelt hat, ein längliches Infusorium, dessen Gestalt wir bei der schon angeführten Abhandlung abgebildet haben. Nach Ausbildung des Infusoriums öffnet sich nämlich die kugelförmige Zelle, und das neue Thier tritt heraus.

Figures supporting the description accompany the paper in *Linnaea*. The earlier paper distinguishes more sharply than the quoted paragraph between observation and interpretation when it comes to the metamorphosis of the organ in question into an infusorium, the author concluding his observations with "So weit meine Beobachtungen," and then proceeds to show that probably the infusoria found about decaying *Spirogyra* originate in the organ described. In view of the prevalence at the time of the doctrine that infusoria take origin in a metamorphosis of decaying plant parts, the attempt to find a connection between the newly discovered organ and the formation of infusoria does not detract from the value of MEYEN'S contribution. Nor is the fact that he speaks of the organ as a "cell" of significance, the term being freely used at the time to designate in a general way any globular or vesicular structure, as well as in the more restricted sense.

It is a curious fact that this work of MEYEN'S has dropped so completely out of the current of citation. In 1830 he reprinted the account, unchanged in essentials, in his *Phytotomie*, under the heading "Thierbildung im Zellensaft."³ In the section of his *Physiology* discussing the nucleus,⁴ he does not refer to this work, but later on⁵ he devotes several pages to it. He has become skeptical whether this organ gives rise to infusoria, but, notwithstanding considerable further study, he was unable to come to a conclusion regarding its nature. SCHLEIDEN had just attracted increased attention to BROWN'S work on the nucleus by the important rôle he ascribed to it in his *Phytogenesis*. MEYEN, attacking his rival's theory, used as one of his arguments that the nucleus is lacking in many tissues. Consistent with this line of thought, mini-

³ *Phytotomie*, Berlin, 1830, p. 165.

⁴ *Neues System der Pflanzen Physiologie* 1:207. 1837.

⁵ *Op. cit.* 3:418. 1839.

mizing the importance of the nucleus, he questions whether the organ he described in *Spirogyra* is BROWN'S nucleus.⁶

SCHLEIDEN, intentionally or otherwise, does not mention this work of MEYEN in his *Phytogenesis* nor in the *Grundzüge*; he names BROWN the discoverer of the nucleus, and this statement in these widely circulated publications is to a great extent the source of the current opinion that BROWN gave the first description of the nucleus.—
W. MARQUETTE, *University of Wisconsin, Madison, Wis.*

NUCLEAR PHENOMENA IN PUCCINIA PODOPHYLLI

(PRELIMINARY NOTE)

In the mycelium of *Puccinia Podophylli* which is to give rise to aecidia and spermagonia a binucleate condition prevails, the nuclei being associated in pairs and dividing conjugately throughout all parts of the mycelium, even before there is any indication of aecidium formation. This condition, however, is not constant. Uninucleate cells are occasionally observed, while those with more than two nuclei are very common.

The aecidium arises in a dense tangle of hyphae beneath the epidermis of the host. Certain cells in the midst of this tangle enlarge and become the "basal cells" of the aecidiospore chains. Whether any one of these cells is simply the enlarged termination of a hypha or is the product of the fusion of two cells, as originally described by CHRISTMAN for certain aecidia of the caeoma type, is not clear. Appearances have been observed which seem to indicate that such a fusion may occur, but any final conclusion upon this point is at present unwarranted. No migrations of nuclei between cells of the same or different hyphae can be recorded. The young basal cells contain two, three, or four nuclei, which at this stage become very large. The very frequent occurrence of four-nucleate basal cells upon a prevailingly binucleate mycelium is a further indication that such cells may not be of simple origin.

The aecidiospores, which are formed with intercalary cells in the usual manner, contain two, three, or four nuclei, depending upon the number contained in the basal cells from which they are derived. In older chains only two of the basal cell nuclei continue to function in this capacity, so that the binucleate spores finally far outnumber the others.

⁶ It is to be noted that vol. I of the *Neues System der Pflanzen Physiologie* was published a year earlier than SCHLEIDEN'S *Phytogenesis*.

The nuclear phenomena in connection with spermatium formation have also been examined. The "basal cells" which bud off the spermatia contain one, two, or even three nuclei. These divide mitotically, providing nuclei for the successively abstricted spermatia. A constriction appears near the tip of the basal cell, and the nucleus passes through the narrow portion into the tip, after which the constriction becomes completed, cutting off a spermatium. In no case did the nucleus appear to be pinched into two parts by the constriction. The spermatia vary in length, some of them being more than three times as long as the diameter of the nucleus, so that they contain much besides nuclear material. In several two nuclei were observed.

A full description of the phenomena outlined above, with figures, will appear in a later paper, together with results of further investigation into the origin of the binucleate condition of the aecidial mycelium.—
LESTER W. SHARP, *The University of Chicago*.

CURRENT LITERATURE

BOOK REVIEWS

An encyclopedia of microscopical technique

In the exact sciences, as a rule, the formulation of a working hypothesis precedes the discovery of methods for its investigation. In biology, on the other hand, this procedure has been often reversed, for here we frequently find that the whole aspect of a science has been changed as a result of new facts brought to light by methods which have been empirically developed. For example, no one could have foreseen that, if nervous tissues were treated successively with solutions of potassium bichromate and silver nitrate, the resulting precipitate of silver chromate would be deposited almost exclusively on the nerve cells and their processes; nor that the medullary sheaths of nerves after long treatment with potassium bichromate would stain strongly in hematoxylin. Yet these two methods have, to a large extent, made possible the modern science of neurology.

The fact that the element of chance has played so large a part in the development of methods for microscopic investigation is doubtless due in part to the lack of adequate training in chemistry and physics of those engaged in microscopical investigation, and to the lack of interest in microscopical structures of those possessing this training; but it is also due in part to the fact that our textbooks of microscopical technique have, for the most part, described the technical manipulations simply as routines to be followed to attain certain results, assuming that the individual using them did not need to know the nature of the reagents he was using, why they were used, nor what each contributed to the final result.

It is sometimes true that careful adherence to an established routine is the safer course for persons of certain limitations in training, but such persons are necessarily limited in their investigative outlook to the exploitation of new material by means of old methods, or to the uncertain hazard of the accidental discovery of new methods. The road to the discovery of new investigative methods by intelligent and well planned experiments is open only to those who are equipped with a knowledge of the chemical and physical properties of the materials with which they are dealing. In this field of experimentation the textbooks of microscopical technique, with one exception, give us but little help. The exception is MANN'S *Textbook of physiological histology*, in which the problems of fixation and staining are fully discussed from the standpoint of the chemistry of the organic materials under investigation, and of the reagents employed. In this work, however, the limitations of theme and space prevented the general application of this method of treatment to the whole field

of microscopic technology, and it remained for the authors of the *Enzyklopädie der mikroskopischen Technik*¹ to make the attempt to provide a comprehensive treatise, in which the whole field of microscopic investigation would be adequately treated from the technical standpoint, and in which, in addition, the chemical and physical properties of the countless reagents employed would receive attention.

The first edition of this work appeared in 1903, and the recent publication of a second edition indicates sufficiently well how great was the demand for such a book. This new edition has been the subject of a thorough revision, bringing all articles up to date and adding many new articles and illustrations. At the same time, a number of articles have been dropped, and others so shortened that the new edition only exceeds the first by some 80 pages. The arrangement of the articles is alphabetical, as the title indicates, and in each case the most significant word has been chosen as the initial word of the title of the article on a given topic. Synonyms appear in the proper alphabetical order, reference being made in each case to the name under which the descriptive article may be found. Much help in locating the various methods is also given by the excellent authors' index at the end of the second volume. After each article numerous references are given which help to enhance the value of the work.

It is to be regretted that more attention has not been devoted to microchemical methods. For example, for the microchemical detection of iron in tissues only MACALLUM's older method of treatment with ammonium sulphide receives attention, and no mention is made of his later methods of unmasking organic iron by means of acid alcohol, nor of his methods of distinguishing between organic and inorganic compounds of iron. The methods for the detection of potassium and of chlorides are not considered at all. In a work of such scope, however, it is inevitable that each investigator working in a special field will find certain omissions and defects, but these are of minor importance when one considers the immense wealth of material which the book offers to the working biologist.—R. R. BENSLEY.

Ancient plants

During the last decade paleobotany has become a transformed subject. The development of a technic for the sectioning of fossil plants, and the recognition of the phylogenetic significance of the vascular system have introduced us for the first time to some real knowledge of ancient plants. To the morphologist this new material has been of immense importance, for it has enabled him to check his conclusions as to evolutionary sequence by the records of history. For the general student of botany it has extended his

¹ *Enzyklopädie der mikroskopischen Technik*. Herausgegeben von EHRLICH, P., KRAUSE, R., MOSSE, M., ROSIN, H., WEIGERT, K. 2. Auflage. Bd. I. pp. 800. Bd. II. pp. 680. Berlin und Wien: Urban & Schwarzenberg. 1910. M 50.

perspective of the plant kingdom enormously. It is high time to present this new field of knowledge to a much larger group than paleobotanists and morphologists, and Miss STOPES has undertaken to do this in her little book entitled "Ancient plants."²

To write such a book is more difficult than to prepare one for special students, for it involves careful selection of material and a simple style. The former always invites the hypercriticism of specialists; and the latter is in danger of sacrificing accuracy to picturesqueness. However, the book is not written for specialists; and extreme accuracy is not so important as vivid impressions. Miss STOPES has certainly succeeded in accomplishing well the task she set for herself. Judgment may vary as to the selections, but this is inevitable; the brevity of treatment has been criticized, but that was a part of the purpose; the attractive and often very picturesque style, even though it might be accused of misleading now and then, is far better for the purpose in mind than a style that flavors of mathematical precision. Such books are intended to arouse interest, and if they stimulate any one to further study, all possible misconceptions will be corrected.

The chapter headings suggest the general treatment: ii, "Various kinds of fossil plants"; iii, "Coal, the most important of plant remains"; iv, "The seven ages of plant life"; v, "Stages in plant evolution"; vi, "Minute structure of fossil plants—likenesses to living ones"; vii, the same—"differences from living ones"; vii-xvii, "Past histories of plant families"; xviii, "Fossil plants as records of ancient countries."

The book can be recommended to all students of botany who should supplement their knowledge of living plants with some information concerning ancient plants. Certainly no student of morphology can afford to neglect the history of his groups, and this little book will serve him well as an introduction.—J. M. C.

NOTES FOR STUDENTS

Mutations in nature.—Mutations probably occur in nature as frequently, in proportion to the percentage of the seeds which succeed in germinating and developing, as in experimental cultures, but actual proof of such mutation must be always wanting. When a single individual of a hitherto unknown type is seen to differ by some marked characteristic from the associated typical individuals of the most closely related species, the natural inference is that the atypic plant is a mutant. If such a plant is found to reproduce its characters in its offspring, such inference is strengthened, but there still remains the question of possible hybridization, and if that can be satisfac-

² STOPES, MARIE C., *Ancient plants; being a simple account of the past vegetation of the earth and of the recent important discoveries made in this realm of nature study*. 8vo. pp. viii+198. *figs.* 122. London: Blackie & Son; and New York: D. Van Nostrand Company. 1910. \$2.00.

torily ruled out, there is the possibility that the form in question is not itself a mutant, but the offspring of a mutant which appeared in some preceding generation. This last question, of course, can never be cleared up in any instance, but is a consideration of no essential consequence. TRABUT³ reports finding near the city of Constantine in Algeria a spineless individual of the wild artichoke (*Cynara Cardunculus*) in an extensive population of the ordinary spiny plants. While considerable variation is found in the vegetative characters of *C. Cardunculus*, no similar individual has ever been reported before. This plant being wholly unarmed would undoubtedly have disappeared undiscovered had it not chanced to grow within the inclosure about the waterworks reservoir of Constantine. The seedlings of this spineless individual have not yet been grown, but it seems probable that it will breed true. There are spineless varieties of cultivated artichokes (*C. Scolymus*), and the possibility of hybridization is not positively precluded, but is rendered less probable by the facts that none of the latter are grown in the vicinity of Constantine and that the new form seems to be typical *C. Cardunculus* in everything but the spines.

Much more important than this supposed mutant of *Cynara* is the discovery of a new form of *Capsella*,⁴ of which a single specimen was found growing among an abundance of *C. bursa-pastoris* at Izeste, Basses-Pyrénées, France. The history of this new species, which is to be known as *C. Viguierei* Blaringhem, parallels that of the celebrated *Capsella Heegeri*, but *C. Viguierei* shows a variation of the capsules in the opposite direction from that presented by *C. Heegeri*. A very large majority of the capsules have four valves of the same general form as those of *bursa-pastoris*, placed at right angles to each other, but the number of valves varies from 2 to 8. Counts of nearly 10,000 fruits, taken at random from plants grown from the seeds of the original specimen, showed the following frequencies: 2-valved, 2; 3-valved, 81; 4-valved, 8450; 5-valved, 301; 6-valved, 288; 7-valved, 24; 8-valved, 16. The new species is normally fasciated, and breeds true to this character as well as to the high number of valves, except when subjected to unfavorable conditions. As grown at Bellevue, France, the leaves of *C. Viguierei* are almost entirely unlobed, while the leaves from a number of pedigrees of *C. bursa-pastoris*, also secured from Izeste and grown under the same conditions, had always the complex lobing characteristic of the reviewer's type *C. bp. heteris*. The author lays particular stress upon the fact that several other species of Cruciferae possess 4-winged capsules. He names several species of *Tetrapoma* which if 2-valved would be classified as *Nasturtium*; *Holar-*

³ TRABUT, L., Sur une mutation inerme du *Cynara Cardunculus*. Bull. Soc. Bot. France 57:350-354. pls. 15, 16. 1910.

⁴ BLARINGHEM, L., Les mutations de la bourse à pasteur (*Capsella Heegeri* Solms, *C. Viguierei*, n. sp.). Bull. Sci. France et Belg. VII. 44:275-307. pl. 6. figs. 10. 1911.

gidium if 2-valved would be a *Draba*; while the Californian genus *Tropidocarpum* has one species with 2-valves and one (*T. capparideum* Green) with 4. Tetracarpellary cultivated varieties of *Brassica* and *Isatis* are also known. Such instances as these, of the recurrence of similar characteristics in more or less closely related species or genera, support the view that variation is definite or "orthogenetic" rather than entirely fortuitous. The author believes that such facts are directly opposed to the older conception that species, genera, and families have a monophyletic origin. On p. 280 the gametic formulae of the reviewer's forms, *Capsella bursa-pastoris tenuis* and *C. bp. rhomboidea*, are transposed; and on p. 304 the date of the discovery of *C. Heegeri* is stated erroneously as 1907 and 1908, the correct dates being 1897 and 1898.—GEO. H. SHULL.

Geotropism and epinasty.—KNIEP⁵ has studied in detail the part played by geotropism and epinasty in the orientation of certain foliage leaves. He makes much use of modified forms of the oblique and intermittent clinostats of FITTING. With these instruments FITTING⁶ answered conclusively many questions on the geotropism of orthotropic organs that two or three decades of work with other instruments had left unanswered. Now, KNIEP proceeds to clear up a number of questions in a plagiotropic organ, the leaf.

In the main *Lophospermum scandens* was used, for the medium-aged leaves of this plant show no sleep movement and little tendency to dark rigor; therefore, they are well adapted to experimentation in darkness. When leaf blades of this plant are placed out of their normal rest position, they recover it by growth-bending of the petiole. During the bending the rate of growth of the middle line is greatly increased. KNIEP designates the usual position of the leaf as the *normal horizontal* position. If the plane of the blade is so changed that the petiole end remains in the original plane but the apical end falls below it, the angle it forms with the normal horizontal position is said to be negative. If this displacement continues -180° , the leaf is then in the *inverse horizontal position*. By a reverse movement from the normal horizontal rest position a positive displacement is brought about. If this displacement continues $+180^\circ$, the *inverse horizontal position* is reached. If in darkness a plant is so tilted that a leaf blade takes a position of $-1^\circ - 114^\circ$, a rapid growth sets up on the morphologically lower side of the petiole (concave bending) and the blade finally acquires its normal horizontal position. If the plant is so tilted that the blade holds any position from -116° to $\pm 180^\circ$, or from $+1^\circ$ to $\pm 180^\circ$, rapid growth begins on the upper side of the petiole (convex bending) and the leaf finally acquires its normal horizontal position. The labile rest position, then, is at approximately -115° .

⁵ KNIEP, HANS, Ueber den Einfluss der Schwerkraft auf die Bewegungen der Laubblätter und der Frage der Epinastie. Jahrb. Wiss. Bot. 48:1-72. 1910.

⁶ Jahrb. Wiss. Bot. 45:675-700. 1905.

When a plant is rotated on an equally rotating horizontal clinostat, a convex curving always occurs regardless of the orientation of the plane of the blade with the axis; this is an epinastic movement. When the plane of the blade is vertical and the midrib horizontal, the leaf is said to be in a flank position; it is evident that there are two flank positions. If a leaf is left in a flank position, the petiole shows both a torsion and a convex bending which finally give the blade the normal horizontal position. By use of an intermittent clinostat which gives repeated 5-15 minute exposures in one flank position followed by equal exposures in the other, all torsion is avoided, but convex curving takes place. The successive flank exposures equalize the effect of gravity and allow epinasty to express itself. By use of the intermittent clinostat, equal exposures between -45° and the two flank positions were given. In this case concave bending occurred, showing that the geotropic stimulus entirely overcame the epinastic; this gives a means of determining the relative strength of the two stimuli. KNIEP puts the question, Can a leaf blade be so oriented on an equally rotating clinostat that concave bending will appear? This is easily accomplished by the use of the oblique clinostat and the combined angles that are possible on it. The great possibility of combinations of angles of geotropic exposure due to variation in obliquity of the clinostat axis and the obliquity of the organ axis with the clinostat axis has been emphasized by FITTING.

This work is the natural outcome of the improved methods that FITTING has given for dealing with problems in geotropism.—WILLIAM CROCKER.

Photosynthesis.—SCHRYVER⁷ believes that he has thrown some light on the mechanism of carbon fixation in green plants. He first describes a modification of Rimini's test for formaldehyde. By the test as modified, 1 p.p.m. formaldehyde gave the reaction, and by proper modification, both free and combined formaldehyde can be detected. Rather accurate quantitative estimates can be made in concentrations varying from 1 part in 100,000 to 1 part in 1,000,000. Films of chlorophyll were formed on glass plates by evaporation of ether solutions. Such plates, exposed to light in the presence of moist CO_2 , showed a marked formaldehyde test; those similarly exposed in absence of CO_2 showed a slight reaction, and those in darkness none. The formaldehyde in plates illuminated in absence of CO_2 was supposed to be formed from CO_2 produced by the chlorophyll film. He believes the formaldehyde formed makes a rather stable compound with chlorophyll, much as it does with amino-containing compounds. He considers the reaction reversible, and represents it as follows: $\text{Chloro}^{\text{H}}\text{H} + \text{HCHO} \rightleftharpoons \text{Chloro}-\text{CH}_2 + \text{H}_2\text{O}$. The removal of CH_2O in sugar formation will cause the reaction to move in the sense of the upper arrow, while accumulation of CH_2O will lead to the reaction moving in the sense of the lower arrow. These results agree with the

⁷ SCHRYVER, S. B., Photochemical formation of formaldehyde in green plants. *Proc. Roy. Soc. London B* 82:226-232. 1910.

view expressed by EULER that the formaldehyde exists mainly in combination, and show why EWART was able to extract formaldehyde from chlorophyll.

BERTHELOT and GAUDECHON⁸ have accomplished some most interesting syntheses and decompositions of chemical compounds by means of the mercury vapor lamp, rich in ultra-violet. All the results indicate the existence of balances in the reactions. Water was synthesized from H_2 and O_2 and decomposed into these elements. Mixtures of CO and O_2 exposed to the ultra-violet produced considerable CO_2 . CO_2 thus exposed gave a slight amount of CO and O_2 . If phosphorus were also present with the CO_2 , a much greater yield of CO resulted, due to the removal of O_2 by phosphorus. If a mixture of CO_2 and H_2 were exposed to the light, considerable formaldehyde resulted. Mixtures of CO and H_2 thus exposed produced considerable formaldehyde. Formaldehyde was decomposed into CO, CO_2 , H_2 , and CH_4 . These results certainly show great possibility in photosynthesis, as the authors use the term, meaning any synthesis by light.

The work suggests the possibility of chlorophyll functioning by transforming the long rays of the red and blue to short ultra-violet rays, which are more effective chemically. This conclusion, however, one should not accept too readily, for GIBSON, working with the leaf, and LÖB, with the effect of silent electrical discharges on solutions of carbonic acid, have shown the possibility of another conception, namely, that the leaf transforms the absorbed light to electricity, which accomplishes the reduction of the carbonic acid to formaldehyde and perhaps the condensation of the latter to sugars. Neither conception is by any means proved; either, however, explains the peculiar fact that red rays (generally ineffective chemically) are very effective in photosynthesis.—WILLIAM CROCKER.

Digestion of sugars.—The tendency to consider enzymes as specific in their activity, and the desire to distinguish enzymes already known and to discover new ones, have often distracted the attention from the more interesting problems in general physiology regarding enzymes. Such a problem is the relation between the enzymes produced by an organism and the utilization of the different substances on which it is able to nourish itself. From this point of view COLIN⁹ makes a comprehensive study of the enzyme activities of the mold *Botrytis cinerea* in the group of sugars. The mold was cultivated on various polyoses, and a study made of the transformations in each case. The enzymes in the culture liquid and mycelium after growth on each sugar was then studied. This was followed by an investigation of the relation which exists between the polyose sugars in general and the enzymes produced by the mold. The mold grew well and showed little morphological variation on

⁸ BERTHELOT et GAUDECHON, Compt. Rend. Acad. Sci. 150:1690-1693. 1910.

⁹ COLIN, H., Hydrolyses de quelques polysaccharides par C *Botrytis cinerea*. Ann. Sci. Nat. Bot. 13:1-III. 1911.

a large number of polyoses. It elaborates various enzymes corresponding to each of these sugars; thus the mycelium thriving on glucose contains sucrase, maltase, etc. A given polyose, therefore, is not indispensable.

The sugar enzymes of *Botrytis cinerea* present two distinct types, based upon diffusibility: the invertase type, perfectly diffusible, and the maltase type, strongly adhering to the pulp. The invertase type includes those enzymes which effect the partial hydrolysis of raffinose, melezitose, gentianose, and stachyose. It is necessary to add emulsin for complete inversion. The enzymes analogous to maltase are lactase, trehalase, melibiase, and in general, those which achieve the complete inversion of trisaccharides and mannietotetrose. The cultures may thus be divided into two corresponding types. The invertase type is characterized by the presence of both the hydrolytic products and the corresponding enzyme in the culture liquid. The maltase type is characterized by the absence of enzyme and hydrolytic products in the liquid. It is necessary to powder the mycelium in order to demonstrate the presence of the enzymes of this type. The type of culture on maltase is very much more general in the case of *Botrytis cinerea*. The cultures on trisaccharides show successively both of the above aspects.

The author draws the following conclusions regarding the specificity of the sugar enzymes of *Botrytis cinerea*: invertase acts as a levulo-polyose, in respect to sucrose, raffinose, gentianose, and stachyose; it produces levulose from each of these sugars either by total or partial hydrolysis; he was unable to characterize a melezitase different from invertase; maltase and lactase are two distinct enzymes; the hydrolysis of trehalose is brought about by an enzyme closely related to maltase; emulsin effects the hydrolysis of gentio-biose; melibiase is clearly distinguished from emulsin, the author being unable to separate it from lactose; it was impossible to identify turanase and mannino-triase with emulsin; from the evidence furnished by *Botrytis cinerea* there is no reason to distinguish them from maltase or lactase.—CHAS. O. APPLEMAN.

Permeability.—In continuing his studies upon modified permeability, CZAPEK¹⁰ reports some most interesting results on the relation between surface tension and modified permeability as brought about by certain aqueous solutions. Various workers have shown a marked agreement between the surface tension and the physiological effect of aqueous solutions of certain non-electrolytes. Passing up the series of mono-alcohols, each succeeding member is (on mol. basis) about three times as effective as the member below it in reducing surface tension of an aqueous solution and in producing certain physiological effects. FÜHNER and NEWBAUER¹¹ have shown for the mono-alcohols, esters, and urethanes that aqueous solutions of equal surface tension produce equal

¹⁰ CZAPEK, F., Ueber die Oberflächenspannung und den Lipoid gehalt der Plasmahaut in lebender Pflanzenzellen. Ber. Deutsch. Bot. Gesell. 28:480-487. 1910.

¹¹ Archiv. Exp. Path. u. Pharm. 56:333-345. 1910.

hemolytic effects. LOEB has shown that for the mono-alcohols the same law holds for induced positive heliotropism and for toxic effects in Copepoda and Daphniidae.

CZAPEK describes a piece of apparatus by which one can determine quickly the surface tension of a solution. He studied the effects of alcohols (primary, secondary, and tertiary), esters, and urethanes upon the permeability of plant cells to certain solutes such as tannins and anthocyanins. Any aqueous solutions of these substances having a surface tension of 0.68 or 0.69 or less (water considered as unity) rendered the plant cells permeable to the contained solutes. The material studied was leaf cells of *Echeveria*, petiole hairs of *Saxifraga sarmentosa*, petals of *Paeonia*, leaf epidermis of *Tradescantia*, etc. CZAPEK believes that the surface tension of the *Plasmahaut* of the cells used is a little more than 0.68 or 0.69, and that as soon as the surface tension of the surrounding solution is somewhat lower, the solutes in the cell begin to pass out. By this means, he states, the surface tension of the *Plasmahaut* can be measured, just as osmotic pressure can be measured, by the use of the ordinary plasmolytic agents. He believes that the *Plasmahaut* is an emulsion of neutral fats. An aqueous emulsion of fats gives a surface tension of 0.68 or 0.69. Lecithin and cholesterol give lower surface tensions and are assumed not to play any rôle in the *Plasmahauten* studied.

CZAPEK emphasizes the fact that permeability is often modified by agents that lower the surface tension but slightly if any, as weak solutions of acids, chloroform, chloral hydrate, etc. This cannot be explained, of course, on the basis of lowered surface tension of the solution. He believes that in the case of acids it is due to the saponifying action of the acid on the fat of the *Plasmahaut*.

On the whole, the article confirms TRAUBE's surface tension theory of osmotic movements of solutions through plant and animal membranes. This theory assumes that the movement of the solutions is in the direction of the lower surface tension.—WILLIAM CROCKER.

Alternative inheritance in elm seedlings.—There are two species of elm in England, *Ulmus montana* and *U. glabra*, both called "Wych-elm," and numerous cultivated varieties of unknown origin which are planted about English hedgerows and parks. Several of these latter are so distinct as to have received specific names, but HENRY¹² finds, as the result of sowing 90 different lots of elm seeds in 1909, that only the two species above named breed true. The seedlings of *Ulmus glabra* have a stiff, erect, unbranched stem with small leaves which are opposite throughout the first season's growth; while *U. montana* has the unbranched stem drooping to one side and only its first two leaves opposite, the rest alternate, the leaves being larger and with longer petioles. All the cultivated varieties of elm tested gave mixtures of seedlings

¹² HENRY, AUGUSTINE, On elm-seedlings showing Mendelian results. Jour. Linn. Soc. Bot. 39:290-300. pls. 5. 1910.

of these two types with respect to the arrangement of the leaves. The Huntingdon elm (*U. vegeta*), commonly believed to be a hybrid, produced 732 opposite-leaved seedlings and 239 alternate-leaved, the expected Mendelian result if the Huntingdon elm is an F_1 hybrid between *U. glabra* and *U. montana*. Other ratios given by different varieties were 245:95 and 310:84, when the parent trees had grown in such situations that their pollination was probably effected by pollen from the same variety. The progeny of a "Jersey" elm, which was probably pollinated by *U. montana*, consisted of 17 opposite-leaved and 19 alternate-leaved, equality probably being "expected." The "English" elm (*U. campestris*) is also an undoubted hybrid, but this rarely produces fertile seeds, though an abundance of samarae are produced; 19 boxes of seeds of the English elm gave no germinations. This sterility and also the appearance of many imperfect flowers in the various cultivated varieties are accepted by the author as additional evidences of hybridity. The author believes that the varieties produced in genera having a number of species are of fundamentally different nature from those in genera including a single species. In birch, oak, lime, poplar, and willow, as in elm, the varieties are hardly to be distinguished from distinct species except by breeding tests. They are generally the result of hybridization, while in the beech and the ash, each of which is represented in northern Europe by a single species, the numerous varieties are of the nature of "sports," whose relationship and varietal value are recognized at once, as in the case of cut-leaved, purple-leaved, weeping varieties, etc.—GEO. H. SHULL.

Geotropism.—ZIELENSKI,¹³ working in JOST's laboratory, has made accurate determinations of presentation, reaction, and critical times, and of the relaxation index in geotropism, using the roots of *Lupinus albus* and *Lepidium sativum*. Use of the clinostat and horizontal microscope renders his methods delicate and accurate, and the paper has the appearance of a real contribution. "Reaction time" is the period (under continual exposure) from the beginning of horizontal placement to the beginning of curvature. "Presentation time" is the least continual horizontal exposure necessary to give curvature at some later time (the organ is on an equally rotating horizontal clinostat from end of exposure to beginning of reaction). "Critical time" is the least exposure that is not entirely nulled by an opposite and immediately following exposure of equal length (organs are on a horizontal equally rotating clinostat after the second exposure). "Relaxation index" is the ratio of the length of the equal individual rotation periods to the length of equal individual exposures (shorter than presentation time), that will not result in summation. Reaction, presentation, and critical times were determined

¹³ ZIELENSKI, FELIX, Ueber die gegenseitige Abhängigkeit geotropischer Reizmomente. Zeitschr. Bot. 3:81-101. 1911.

by reaction in more than half the roots, and relaxation index by reaction in fewer than half. The accompanying table from the article summarizes the results:

	Presentation time	Critical time	Reaction time	Relaxation index
Lepidium sativum at 17-18C. .	5.5 min.	6 min.	25.5 min.	30
“ “ at 25-27C. .	1.5 “	2 “	12.5 “	40
Lupinus albus at 17-18C. .	8.5 “	11 “	46.5 “	20
“ “ at 25-27C. .	2.0 “	7 “	33.0 “	25

One is struck here by the time demanded for relaxation from an exposure; it is very much greater than reported by FITTING. The author attempted, without full success, to develop a formula by which any one of the critical periods can be calculated from the other three.—WILLIAM CROCKER.

Photosynthesis.—LUBIMENKO¹⁴ finds that there is a light optimum for the production of dry substance by green plants. The absolute value of this optimum is less than that by which the chlorophyll apparatus is able to furnish the maximum of photochemical work expressed in the decomposition of CO₂. By means of monochromatic filters and gasometric determinations, a comparison is made of the action of the different colored rays on the decomposition of CO₂. These results are compared with the action of the same rays on the production of total dry weight. The energy for CO₂ decomposition in colored light depends upon the absorption of the various colored rays by the chloroplasts as well as on their caloric energy. The author objects to the method employed by KNIEP and MINDER and others in determining the influence of different colored rays on CO₂ assimilation, on the ground that they measured the quantity of light falling upon the leaf and not that absorbed by the chloroplasts. The real carbon fixation expressed by the increase in dry weight is influenced unequally by the different colored rays. The maximum increase in dry weight occurs under the action of the blue-violet rays. The yellow-orange rays are inferior to the red rays, and the minimum occurs in the green rays. It is necessary to assume two successive stages in the photosynthetic process. The first is characterized by the decomposition of CO₂ and synthesis of the first organic product. In this stage of the process the plant utilizes predominantly the energy of the red rays of the solar spectrum. The second stage is characterized by the definitive fixation of the first organic product, and the plant employs for this work especially the blue-violet rays.—CHAS. O. APPLEMAN.

¹⁴ LUBIMENKO, M. W., L'assimilation chlorophyllienne et la production de substance sèche à la lumière blanche et à la lumière colorée. Rev. Gén. Bot. 23: 1-14. 1911.

Light measurements.—Following the well known methods of WIESNER, several careful investigations by RÜBEL have largely increased our knowledge of light conditions in alpine and desert regions and at sea. The most prolonged of these studies was made at Bernina Hospice,¹⁵ a station in the Alps with an elevation of 2309 meters, where it has been clearly demonstrated that both the maximum light intensity and the light totals are greater than those for lower altitudes. The minimum light intensity at midday in the Alps is much higher than at Vienna, the ratio being 85:7; while a similar relation exists between the light totals. Other interesting items from the abundant data are the nearly equal values of direct and diffuse light during the growing period, the somewhat increased light intensity after precipitation, and the decidedly greater available light on southern as compared with northern slopes. Many of these data may prove valuable in interpreting alpine vegetation.

Observations made at sea¹⁶ tend to show that the maximum light intensity differs little from those of regions of low altitude on shore, but that the amount of diffuse light is somewhat greater. The characteristic of desert light conditions¹⁷ appears to be the low light intensity both at full sunlight and with cloudy sky, an intensity which increases considerably, however, immediately after rainfall. This must have some influence in modifying the otherwise extremely xerophytic conditions, but the author seems to follow other investigators of light phenomena in failing to recognize the influence of light upon transpiration.
—GEO. D. FULLER.

Work at Peradeniya.—The numerous publications issued from the Royal Botanic Gardens at Peradeniya indicate great activity, which naturally expresses itself chiefly in investigations connected with economic plants. T. PETCH, the mycologist, has found a very fruitful field for cultivation; recent *Circulars* dealing with "Brown root disease" (*Hymenochaete noxia*), which attacks several of the most important plants; "A root disease of *Hevea*" (*Sphaerostilbe repens*), the Para rubber plant; "Root diseases of *Acacia decurrens*," a plant extensively used as a wind-break for tea or for "green manuring"; "Root diseases of tea"; and "Cacao and *Hevea* canker." In the *Annals*, the same author has presented a study of *Lasiodiplodia*,¹⁸ showing in a striking way the confusion that has arisen among the subgenera of *Diplo-*

¹⁵ RÜBEL, E., Untersuchungen über das photochemische Klima des Berninahospizes. *Viertel. Natf. Gesell. Zürich* 53:1-78. 1908.

¹⁶ ———, Beiträge zur Kenntnis des photochemischen Klimas der Canaren und des Ozeans. *Idem* 54:289-308. 1909.

¹⁷ ———, Beiträge zur Kenntnis des photochemischen Klimas von Algerien. *Idem* 55:91-102. 1910.

¹⁸ PETCH, T., On *Lasiodiplodia*. *Ann. Roy. Bot. Gard. Peradeniya* 4:445-465. 1910.

dia; and also a study of *Thielaviopsis paradoxa*,¹⁹ recently found to be the cause of a stem disease of the cocoanut palm in Ceylon.

In other *Circulars* issued during the latter part of 1910, E. E. GREEN presents a "Report on the outbreak of *Achatina fulica*," a ravaging snail; M. KELWAY BAMBER and R. H. LOCK discuss "The effect of different intervals between successive tappings in Para rubber (*Hevea brasiliensis*)"; Reports on "Cotton growing in Ceylon" and on "*Cymbopogon* grass oils in Ceylon" are published; and Director J. C. WILLIS presents the first of a series of directions as to "School gardening and nature study." WILLIS²⁰ has published also the first instalment of a revision of the catalogue of the vascular plants of Ceylon, published by TRIMEN in 1885.—J. M. C.

Effect of strontium salts on algae.—The chemical properties of calcium and strontium agreeing more closely than those of sodium and potassium, one might expect to easily substitute strontium for calcium in physiological relations. Investigations along the animal side have been to the contrary, and LOEW²¹ has endeavored to gain further knowledge by tests with species of *Spirogyra* especially. Chemically equivalent solutions of calcium chloride (1 per cent) and strontium chloride (1.7 per cent) were used separately. The filaments remained for months in the calcium chloride practically intact. In the strontium chloride the injurious effects were manifested slowly, but within a month the chloroplasts became yellowish-green, less active in starch-making, and finally the cells died. In the strontium solution needle crystals developed in the cells, something which did not occur in the calcium solution. It appears obvious to the author that such crystals represent a combination of strontium with organic acid. Since the algae endure the strontium salt longer than any other except calcium, it seems that strontium does not rapidly displace from important positions in the protoplasm other metallic elements such as potassium and magnesium. According to the law of mass-action such a displacement would be expected. A discussion of why strontium does not physiologically replace calcium leaves the reader with little to cling to.—RAYMOND H. POND.

Anatomy of Riccia.—Taxonomists separate the genus *Riccia* into two subgenera, *Euriccia* and *Ricciella*. In the former the dorsal region of the thallus consists of columns of cells split at the corners, each 4 columns of cells thus inclosing a long narrow air chamber having no lateral communications; in the latter, flat lamellae bounding the relatively large air chambers. STEPHANI, however, studying *R. vesiculosus*, in which 8 cells bound the air chamber, places this form in the subgenus *Ricciella*, and says: "Dividing the genus into

¹⁹ PETCH, T., *Thielaviopsis paradoxa* (de Seynes) v. Höhnelt. *Idem* 511-574.

²⁰ WILLIS, J. C., A revised catalogue of the flowering plants and ferns of Ceylon. *Idem* 467-510.

²¹ LOEW, OSCAR, Ueber die Wirkung von Strontiumsalzen auf Algen. *Flora* 102: 96-112. 1911.

two parts is hardly justifiable, where, as this plant shows, intergradations exist."

JUEL,²² studying *R. Bischoffii*, found that the cells of the median dorsal region of the thallus are arranged according to the so-called *Euriccia* pattern, while the wings have the *Ricciella* pattern; the smallest air chambers being bounded by 6 cells and the largest by 15. He attributes the presence of the 4-sided air spaces of the middle region to the fact that the ventral cells grow a little more rapidly than do the dorsal cells. The increasingly larger air spaces of the wings are due to very unequal growth of the cells. This work is another example of how artificial and arbitrary distinctions frequently break down when the problem is attacked by an observer trained in morphological methods.—W. J. G. LAND.

Traumatotaxy and chemotaxy.—RITTER²³ has published an article on traumatotaxy and chemotaxy of the nucleus. It adds little that is new and is not markedly critical. In the region of the wound the nuclei in the intact cells move toward the wound and enlarge somewhat. Light and gravity do not modify the reaction, while absence of oxygen and anaesthetics entirely stop it. After five or six days the nuclei recover their normal position; this agrees with the duration of the respiratory acceleration due to wounding. There are a number of parallels between the traumatotactic and chemotactic responses, but the author concludes that the chemotactic effect of endosmosing solutes from the dead cells cannot account for any considerable part of the traumatotactic response. The wound response is much more rapid than the response to chemicals; wounds also produce protoplasmic movements, while the chemicals do not. RITTER believes that in the wound response the nuclei are passively transported by the moving protoplasm; on this point his evidence is certainly not convincing. The effective chemotactic substances were salts, bases, organic acids, and carbohydrates. Inorganic acids and many organic substances were not effective.—WILLIAM CROCKER.

Hybrids at Kew.—A list²⁴ of all hybrids produced in the Royal Botanic Gardens at Kew, England, will surprise many by its shortness, considering the length of time during which Kew has been one of the great botanical clearing houses of the world, and the obvious advantages it has had on this account for the production of hybrids. The earliest hybrid produced at Kew was the result of a cross between *Rhododendron Griffithianum* and *R. Hookeri*, made in 1874; and in the 36 years from that time, until this list was published, 49 hybrids have been produced, and 12 failures are reported.

²² JUEL, O., Ueber den anatomischen Bau von *Riccia Bischoffii* Hub. Svensk. Bot. Tidsk. 4:160-166. pl. 7. figs. 5. 1910.

²³ RITTER, GASTON, Ueber Traumatotaxis und Chemotaxis des Zellkernes. Zeitschr. Bot. 3:1-42. 1911.

²⁴ Hybrids raised at Kew. Kew Bull. 1910:321-328.

The largest number of hybrids secured in any one year were 6, produced in 1898. It is disappointing to the hybridologist to find in this list almost no data of any scientific significance regarding these hybrids. The brief comments made in connection with each cross refer purely to the value of the result for decorative or other economic purposes, and no definite comparison is made between the characters of the hybrid and those of its parents, except occasionally in regard to cultural matters.—GEO. H. SHULL.

Position of Gnetales.—LIGNIER and TISON²⁵ have applied their anatomical methods to the so-called “flower” of the Gnetales, and have reached the conclusion that the group belongs to angiosperms, among the Amentales; and that it probably represents a reduction series derived from the “base of the angiosperm trunk.” This carries one back to the old conflict over gymnospermy; and in fact the interpretation of the ovule of Gnetales is almost identical with that of the ovule of gymnosperms nearly 100 years ago, for it reads “un ovaire fermé, prolongé en style et stigmate et ne renfermant qu’un seul ovule réduit au nucelle.” This conclusion is a good illustration of the use of selected testimony rather than of all available testimony; an eclectic rather than a synthetic judgment. One might imagine a reduction series resulting in an open ovary, for there are open ovaries among angiosperms; but that such a series could result in the reappearance of such structures as archegonia, etc., is beyond the reach even of scientific imagination.—J. M. C.

Cytase and cytoagulase.—GRÜSS²⁶ continues his studies upon gum-formation in the cherry and peach. He attributes it to the action of cytase upon the hemicellulose (especially galactans) of the secondary layer of wood vessels. Quantitative analysis shows 4 per cent of the wood vessels to be galactans. Excessive gumming he attributes to abnormally high cytase action. In the spring, when there is a general digestion of the reserved materials, he could detect a dissolution of the secondary layers of the wood vessels in the neighborhood of the cambium. Cytase was also abundant in this region and the vessels were filled with gum. In autumn he finds in the cambium region an enzyme which deposits an insoluble product from the gum, which gives the reactions of hemicellulose; he calls this condensing enzyme “cytoagulase.” The papers of GRÜSS are thrown together in such a way that careful perusal leaves one in doubt as to his exact meaning.—WILLIAM CROCKER.

Germination.—GASSNER²⁷ continues his studies on the germination of the South American grasses, the present paper reporting on *Stenotaphrum gla-*

²⁵ LIGNIER, O., et TISON, A., Les Gnétales sont des Angiospermes apétales. Compt. Rend. Acad. Sci. Paris **152**:201-204. 1911.

²⁶ GRÜSS, J., Ueber das Verhalten von Cytase und Cytokoagulase bei Gummibildung. Jahrb. Wiss. Bot. **47**:395-430. 1910.

²⁷ GASSNER, GUSTAV, Ueber Keimungsbedingungen einiger südamerikanischer Gramineensamen. Ber. Deutsch. Bot. Gesell. **28**:504-512. 1910.

brum and *Paspalum dilatatum*. In the former light is not necessary for germination; but it shortens the required "after-ripening" period and increases somewhat the percentage of germination. For complete "after-ripening" 30 or more weeks of dry storage are required. A period in a seed bed at low temperature does not favor germination. In *P. dilatatum* 1 or 2 weeks at 50–60° C. dry storage brings about after-ripening. A period in the seed bed at low temperature is effective if it follows 20–30 weeks of dry storage. In this species light does not favor germination. This paper, as did the earlier one,²⁸ shows lack of exact analytical methods.—WILLIAM CROCKER.

Embryo sac and embryo of Clematis.—SOUÈGES²⁹ has undertaken the investigation of the embryo and embryo sac of the Ranunculaceae, the four parts cited dealing with the Clematideae. The general situations in the family are well known, so that the usefulness of the present account consists in the elaboration of the details of a single tribe, presumably to be followed by similar accounts of other tribes. Perhaps there is some over emphasis of a definite sequence of stages in embryo-formation, for cell-successions have proved to be quite variable, and such uniformity as can be observed is probably an indication of the uniformity of conditions in which the successive divisions occur. There is certainly evidence of a lack of familiarity with the literature of the subject.—J. M. C.

The embryo of the Bromeliaceae.—GATIN³⁰ has investigated the structure of the mature embryo and the germination of representatives of the Bromeliaceae. The three tribes were represented by a species from each of the following genera: *Karatas*, *Billbergia*, *Aechmea*, *Puya*, and *Tillandsia*. The variations uncovered are so considerable, and so doubtful as to their significance, that no general conclusion can be reached. The paper, therefore, is a contribution of facts that may become of service.—J. M. C.

Light a form-stimulus.—DUBARD and BUCHET³¹ believe that light intensity determines the nature of the relief configuration of the hymenial surface of *Merulius lacrymans*. In high light intensity the surface shows high irregularly anastomosing ridges and deep depressions. In low intensity the furrows and ridges are less marked, and are arranged parallel to the incident rays of light.—WILLIAM CROCKER.

²⁸ BOT. GAZETTE 51:76–77. 1911.

²⁹ SOUÈGES, E., Recherches sur l'embryogénie des Renonculacées. Bull. Soc. Bot. France IV. 10:242–250, 266–275, 509–517, 569–576. figs. 56. 1910.

³⁰ GATIN, C.-L., Premières observations sur l'embryon et la germination des Broméliacées. Rev. Gén. Botanique 23:49–66. figs. 32. 1911.

³¹ DUBARD, M. M., et BUCHET, S., De l'action de la lumière sur le *Merulius lacrymans*. Bull. Soc. Bot. France 57:417–420. 1910.

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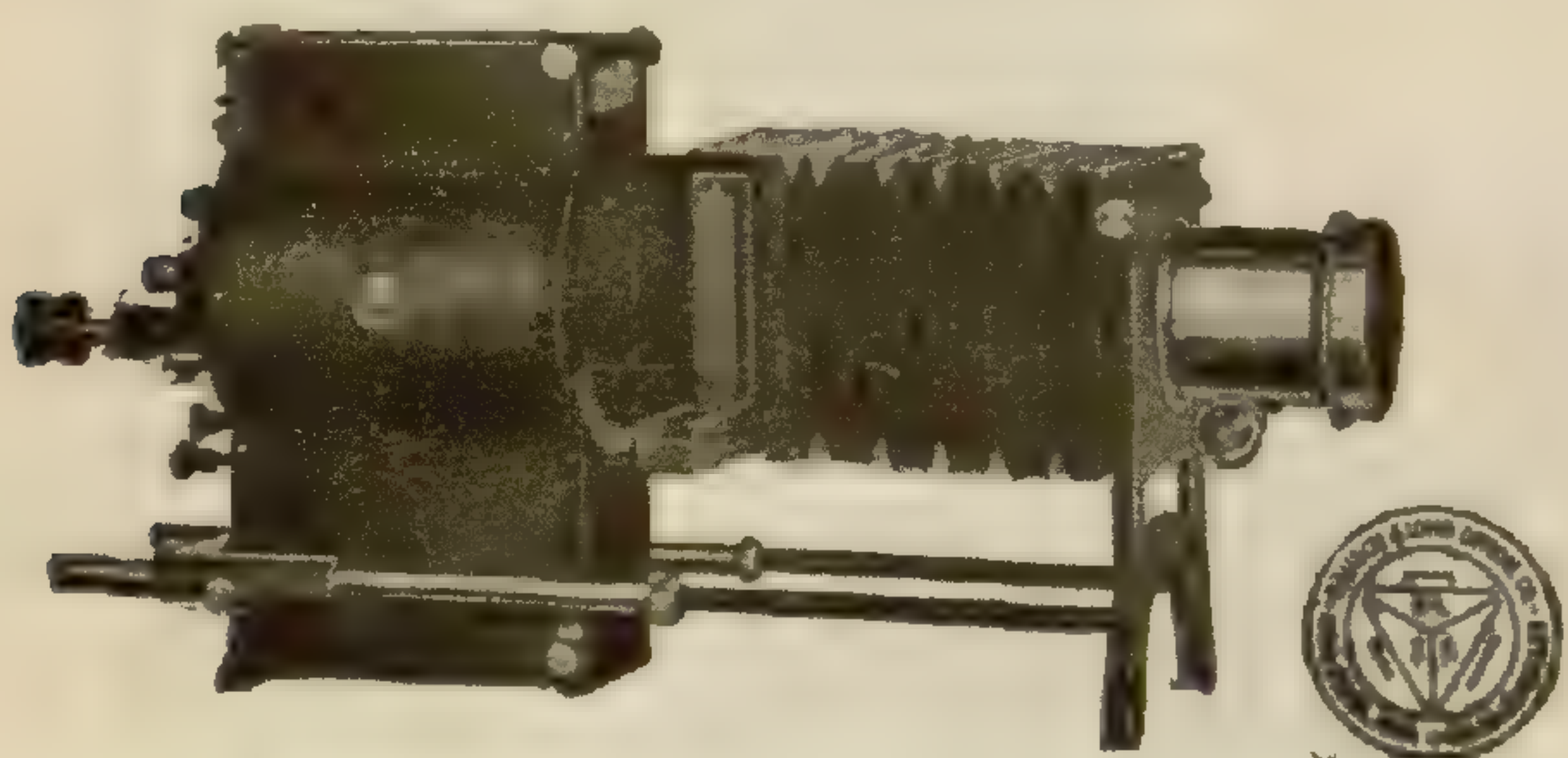


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